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Have wolves (*Canis lupus*) finally scared moose (*Alces alces*) in Sweden?

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Have wolves (*Canis lupus*) finally scared moose (*Alces alces*) in Sweden?

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Summary

Predators can impact prey animals by reducing their numbers in an area through attacking and killing them but also by chasing and scaring them. Scaring prey does not necessarily end in the death of the individual prey animal and the number of prey does not need to dramatically change, but the location of individual prey animals may change. If predators cause the prey to change how they behave it is known as an indirect effect of predation. Indirect effects of predation can result from predators attacking animals in certain areas which causes the prey to avoid those areas. Predation risk is an important aspect to consider when studying predator-prey ecology. If prey avoid certain environments it gives the vegetation, usually eaten by the prey animals, a chance to grow and could eventually lead to the land changing from a more open area to a more forested area.

My study aimed to look at whether wolves have caused an indirect effect on moose in Sweden, within an area dominated by human land use. I looked at the distribution of moose faeces and moose browsing damage across a research area in South central Sweden (Grimsö Wildlife Research Area), to see if it changed between years without wolves (1997-2003) and years with wolves (2004-2016). I was interested to see if moose would reduce the use of areas where the chance of wolf attacks was greater. Open habitat, namely bogs and clear-cut areas, appear to have a greater chance of wolves killing moose. I therefore used bogs and clear-cuts as a risky environment and compared moose faeces and browsing damage in the open areas against faeces and browsing found in dense young forests and older forest. I increased my scale of detail in the study by also looking at how far away I found moose faeces and browsing damage from forested areas in-case wolves have altered moose behaviour so they now stay closer to covered environments.

Within ecological studies many aspects of an animal's environment can impact how it behaves and so it is important to include elements of the animal's environment to paint a more realistic picture of what is affecting the animals. I therefore included snow depth data, food availability data and road data alongside my main focus of wolf presence to see which characteristics are most important in explaining how moose use their habitat.

My results did not find a strong effect of wolves on moose behaviour, which is similar to previous studies within Scandinavia on wolf and moose interactions. I did find a change in how moose have been selecting habitat after wolves returned but it was not a dramatic shift from one habitat type to another. The result likely reflects how the amount of food within the moose environment has changed since wolves returned. As different amounts of habitat types change it can impact how the moose select areas in a so-called functional response. The area is dominated by forest management actions and as a result the forest can be cut down or thinned out from one year to the next affecting the amount of food for moose to eat.

A great deal of interest has occurred on the indirect effects of predation since the reintroduction of wolves to Yellowstone National Park in North America. The wolf

has been linked to far reaching effects, called trophic cascades, such as allowing other animals such as song birds and beavers to return to areas that now offer more vegetation for cover and forage, as the ungulate community has been reduced in size and changed its foraging behaviour.

Although the Yellowstone results are compelling, and have been reproduced in other areas such as Banff National Park, there has been a criticism that indirect effects of predation are seen mainly within national parks. When we look for them in areas more impacted by human activity we find a variety of different results that make it difficult to conclude on the role of predators in their environment. In Sweden the inability to find an indirect effect of wolves on moose could be due to a high hunting pressure on moose by humans as well as a low chance of individual moose actually meeting a moose. A low encounter rate means moose do not have a large selection pressure to change how they select their habitat from a wolf predation point-of-view.

In todays social landscape of rewilding certain habitats and environments the idea of reintroducing large carnivores is often discussed. If deer populations can be controlled naturally by carnivores then less hunting by humans needs to occur. If deer populations avoid certain areas through fear of predation then industrial forestry may benefit as the damages by deer could be reduced in particular areas. My results do not show this trend and indeed highlight the variability found within the more human dominated landscapes we can find within Europe. Such variability means we need to be careful before saying apex predators will generate a host of positive effects if reintroduced to an area.

Abstract

Carnivores are coming back to Europe and the repercussions of their return on prey species is not fully understood. Research from North American studies suggests predators can indirectly affect how ungulates will select their habitat which can result in a change in vegetation growth as browsing pressure is relaxed in risky areas. The highly human dominated landscapes of European countries could limit the effect predators have, as humans alter so much of the environment, from forestry to hunting. I use resource selection functions to analyse 20 years of data collected in the Grimsö Wildlife Research Area (140 km^2), in a before/after study design to see if the return of the wolf (*Canis lupus*) in Scandinavia has caused moose (*Alces alces*) to change how they select winter habitat. I show a change in moose habitat selection after wolf recolonization, but find no conclusive evidence of an indirect effect of wolves. A more likely explanation for the observed changes in moose habitat selection within the Grimsö Wildlife Research Area is a functional response between moose and forage availability.

Have wolves (*Canis lupus*) finally scared moose (*Alces alces*) in Sweden?

Introduction

Background to the indirect effects of predation

The idea that apex predators can exert a top down control on their ecosystem has generated controversy and interest within parts of the scientific community and general public, noticeable through the popularity and general discussion around the video, "How wolves change rivers" [1, 2]. The numbers of herbivores present in an area, the apparent natural regeneration of vegetation, and available forage for herbivores are all factors possibly linked to the effect carnivores produce on their prey, in a so-called trophic cascade (Estes *et al*, 2011). The removal of large predators from food webs and subsequent species composition changes has been documented in terrestrial (Morris and Letnic, 2017) and aquatic (Estes *et al*, 1995) ecosystems. The effect a predator has on its prey can be direct, through the reduction in prey density and thus less mouths feeding directly on plants, or indirect through prey behaviour changes due to predation risk, and thus a change in where and when prey feed in/on certain plants (Lima and Dill, 1990).

To reduce the risk of predation, prey have developed multiple strategies for avoiding predators such as increasing vigilance (Hunter and Skinner, 1998, Halofsky and Ripple, 2008), changing habitats (Creel *et al*, 2005a, Edwards, 1983) and forming groups (Lipetz and Bekoff, 1982). Anti-predator strategies take time away from feeding or place ungulates in areas of lesser forage quality. The effects of predation risk can have long term negative effects by, for example, impacting the reproduction of ungulates (Creel *el al*, 2007). A trade-off must be made in balance with the energy requirements needed to sustain life (Brown *et* al, 1999).

Predation risk is believed to produce a landscape of fear, from which prey will change their behaviour in an attempt to reduce the risk of being eaten (Lima and Dill, 1990). The basis of the landscape of fear is that the risk of predation varies in space and time and prey species will take risk into consideration when selecting habitat for different activities (Laundré *et al*, 2010).

If behavioural mediated effects occur as a result of predator presence (Preisser *et al*, 2005) then prey species will experience a trade-off between when to hide and when to forage, and in what areas, based on the perceived level of risk (Lima and Dill, 1990). For example, if predators exist in an area it may be safer to stay away from risky places, however if those risky places provide the most optimal supply of forage then gaining food in these patches may become more important (Brown *et al*, 1999). If ungulates decide to avoid certain areas it indirectly impacts the vegetation as these areas will receive less browsing, such as is seen in a presence/absence study on cougars (*Puma concolor*) in Utah USA (Ripple and Beschta, 2006). Areas with

[1] https://www.youtube.com/watch?v=ysa5OBhXz-Q *The original video, showing nearly 40 million views, as of August 2018.*

[2] https://www.accuweather.com/en/weather-news/scientists-debunk-myth-that-yellowstone-wolves-changed-entire-ecosystem-flow-of-rivers/70004699 *A follow up blog arguing against the role of the wolf. Many comments are negative towards the article, Accessed August 2018.*

cougars resulted in better recruitment of young hydrophytic plants as browsing levels were reduced.

Most studies on the indirect effects of terrestrial carnivores on their prey come from North America. For example it has been shown that elk (*Cervus canadensis*) reduce their use of open areas when wolves (*Canis lupus*) are present due to an apparent increased risk (Creel *et al*, 2005a, Kunkel and Pletscher, 2000) and aggregate more when in open habitats (Proffitt *et al*, 2009). Wolves have, by some researchers, been considered a catalyst to restoring ecosystem health due to their effects on elk and the corresponding release of plants from browsing (Ripple and Beschta, 2012). Within Banff Nation Park, Canada, it has been shown that wolves impacted elk survival leading to a recovery among willows that in turn allowed beavers (*Castor canadensis*) to increase in number (Hebblewhite *et* al, 2005).

There is however a growing body of work which is beginning to question whether wolves are actually causing such large-scale cascading events as depicted from some research groups (Marris, 2018). Tercek *et al* (2010) showed that abiotic factors such as water availability and primary productivity were important in the development of vegetation growth. Creel and Christianson (2009) showed that snow was most important for controlling willow (*Salix Spp.*) growth and wolf presence actually increased willow browsing, the opposite of expected. Ford and Gohenn (2015) conclude that there is a lack of scientific replication on the studies showing positive effects of vegetation growth after wolf return. Creel and Winnie (2005b) show that wolves were not the reason for their observed response of grouping in elk but more likely the distribution of resources. Moreover, Kuijper *et al* (2016) highlight that many of the studies completed so far are biased to North American ecosystems, and further biased to areas within national parks and protected lands. A study completed in North America outside a national park concluded that human activity was a more important driver of ecosystems than carnivores (Muhly *et al*, 2013). The generality of results therefore is questionable and warrants further investigation before the information is used for management decisions in other systems.

A European context

Carnivores are making a comeback across Europe (Chapron *et al*, 2014), and compared to North America, knowledge of the indirect effects carnivores have on their prey is lacking (Kuijper, 2011). European landscapes are dominated by human management (Linnell *et al*, 2005), with agricultural development and dense infrastructure (Basille *et al*, 2009). European settlers had a greater ability to alter the land than North American areas (Kay, 1994). As human impacts occur at all levels of the ecosystem they may also influence the way carnivores and ungulates can interact (Ordiz *et al*, 2013), such as by causing disturbance levels which restrict carnivore distribution (Llaneza *et al*, 2012). The call that wolves could be an important player within conservation programs (Ripple and Beschta, 2012) and for managing forest damages (Bojarska *et al*, 2017) means it is important to fully understand the role carnivores will have on their prey, in more human dominated environments, outside of national parks.

Within the European context predator-prey interaction studies have shown variable results and while Theuerkauf and Rouys (2008) found no effect of wolf predation

risk on red deer or roe deer (*Capreolus capreolus*), Tinoco Torres *et al* (2011) observed roe deer selecting dense habitat and linked it to an anti-predator strategy. Kuijper *et al* (2014) did not find an effect of habitat but found that red deer increased vigilance when they detected the odour of wolves. Theuerkauf and Rouys (2008) also stated that human impacts from hunting and forestry will control the system much more than large carnivores, something backed up by Tinoco Torres *et al* (2011) who showed that roe deer also avoided roads to elude humans.

The variability within European studies on predator-prey interactions show the need for more research, and in particular, spanning different areas of Europe. The recolonization of wolves within Scandinavia (Wabakken *et al*, 2001) has provided a unique opportunity to study the role a predator can have on the behaviour of its prey in an anthropomorphic environment.

So far Scandinavian studies conducted on moose (*Alces alces*) habitat selection (Nicholson *et al*, 2014), moose grouping behaviour (Månsson *et al*, 2017), hunting success on moose (Sand *et al*, 2006), and moose movement patterns (Wikenros *et al*, 2016) show little evidence that the wolf has caused behavioural changes to its prey.

Eriksen *et al* (2011) concluded that a future study looking at how ungulates behaved before and after wolves returned to an area would be of great interest to try to uncover the role of the wolf within Scandinavia. It is possible that previous studies on habitat selection have not been detailed enough and that a finer-scaled study may better illuminate how the wolf has affected the behaviour of its prey (Nicholson *et al*, 2014).

Aims and hypotheses

In my study I have concentrated on fine-scaled habitat selection of moose in a before and after design based on wolf recolonization of an area in south-central Sweden. I have focused on the idea that a landscape will provide both risky and refuge areas for its herbivorous species (Hebblewhite *et al*, 2005, Kauffman *et al*, 2007) that may affect the spatial distribution of the wolves' main prey, moose, and their browsing pattern. I investigated whether the return of wolves to this human modified landscape have impacted on moose habitat selection. The study was made possible due to a 20-year data collection effort on moose density, distribution, and browsing impacts on preferred forage species during winter that spans both before and after wolves colonised the local research area (Long term data was available through the Swedish Infrastructure for Ecosystem Science (SITES)[3]). I also gathered data on snow and distances to roads which could be important in describing moose habitat selection. When snow ground cover exceeds 10cm it has been shown to impact moose habitat selection as the potential forage from the field layer is covered (Månsson, 2009). In addition, roads can cause disturbance to moose (Dussault *et al*, 2007) but also result in increased foraging, which could influence where moose decide to feed (Bowman *et al*, 2010).

As wolves appear to prefer moving along linear features (Bergman *et al*, 2006) it is possible that being close to edges in habitat types could drive fear, as seen with proximity to streams and roads (Kauffman *et al*, 2007). Risky areas can be defined

[3] *http://www.fieldsites.se/en-GB/about-sites/field-research-stations/grims%C3%B6-32652353*

as areas where wolves more frequently kill their prey successfully which in the Scandinavian system, appears to be more open habitats (Gervasi *et al*, 2013).

Based on Johnson (1980) animal use of space encompasses both food type consumed and habitat type selected. I completed a habitat selection analysis using two indices of selection; the presence and absence of moose pellet groups and the presence and absence of moose browsing on pine. I tested the effect of wolf presence by exploring whether the probability of presence of moose pellet groups and pine browsing within certain habitats changed after wolves returned to the area.

Many studies on predation effects begin by generating a landscape of risk prediction map based on wolf GPS locations to use as a wolf risk parameter (Hebblewhite and Merill *et al*, 2009, Kuijper *et al*, 2013). There are studies however which say it is not the actual location of wolves that is important for inducing fear in ungulates but more the simple knowledge that a predator is in the area in combination with the spatial heterogeneity provided by the landscape (Hebblewhite *et al*, 2005, Kauffman *et al*, 2007, Bojarska *et al*, 2017). Vulnerability of prey does not always correlate with density of prey such that certain areas may be more dangerous than others (Bergman *et al*, 2006). I decided to avoid using a predation risk map of wolf density and, more simply, I looked at the time frame before and after wolf recolonization. The idea being that moose will recognise that wolves are present in the landscape and adjust their behaviour, not in relation to the highest wolf density areas, but in relation to the riskiest areas.

The risky nature of open habitats in Scandinavia is backed by the literature showing ungulates avoiding open areas in the presence of wolves (America (Kunkel and Pletscher, 2000), Europe (Tinoco-Torres *et* al, 2011)). I therefore hypothesise that open areas will constituted a higher risk of wolf predation than densely covered areas and predict that:

1) The probability of finding moose pellet groups in open habitats will be reduced after wolves return, and;

2) The probability of pine browsing will decrease in open areas after wolves return with a reduction in pine browsing probability with increased distance from more densely covered areas.

Methods

Site description

Data was collected within the Grimsö Wildlife Research Area (140 km^2) located in the counties of Västmanland and Örebro in South-Central Sweden (59-60°N and 15-16°E, figure 1). The area is situated in the southern boreal zone and exhibits average January temperatures of -4°C to -6°C and average July temperatures of 15°C to 16°C (Wastenson *et al*, 1995). Winter usually begins in December with the onset of spring in late March (Wastenson *et al*, 1995). Summer conditions occur from the start of May until September (Wastenson *et al*, 1995). Average precipitation is 600-700 mm with 180-210 mm falling as snow, with an average yearly snow depth of 20-30 cm (Wastenson *et al*, 1995). The land is mainly composed of forests (78%) and

interspersed with bogs (8%), lochs and rivers (8%) and farmland and meadows (8%), with an elevation of 100 to 150 meters above sea level (Nicholson *et al*, 2014).

The forest consists mainly of Norway spruce (*Picae abies*) and Scots pine (*Pinus sylvistris*) intermixed with the deciduous trees rowan (*Sorbus acuparia*), aspen (*Populus tremula*), birch spp *(Betula pubescens* and *Betula pendala*) and willow (*Salix* spp.) as well as juniper (*Juniperis communis*) (Månsson *et al*, 2007). The field layer is a composition of bilberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-abaea*), heather (*Culluna vulgaris*) and wavy hair grass (*Deschampsia flexuosa*). The land is mainly owned by a state-owned forest enterprise company called Sveaskog (Månsson *et al*, 2011) and intensive active forest management occurs with a turnover of stands being roughly 100 years (Swenson and Angelstam, 1993). Forest stands range in size from 0.5 hectares (ha) to 64 ha with an average size of 6 ha (Månsson *et al*, 2007).

An aerial count of moose in the area was conducted in 2002 showing 1.2 moose per km^2 and again in 2006 showing 0.8 moose per km^2 (Rönnegård *et al*, 2008). Roe deer are also present with a population of 5 per km^2 in 2005 (Rönnegård *et al*, 2008). There is also a small population of wild boar (*Sus scrofa*) in the area (Nordström *et al*, 2009). The first wolf territory in the research area was established during the winter of 2003/2004 and there has been a continued presence of territorial wolves since then (Nicholson *et al*, 2014).

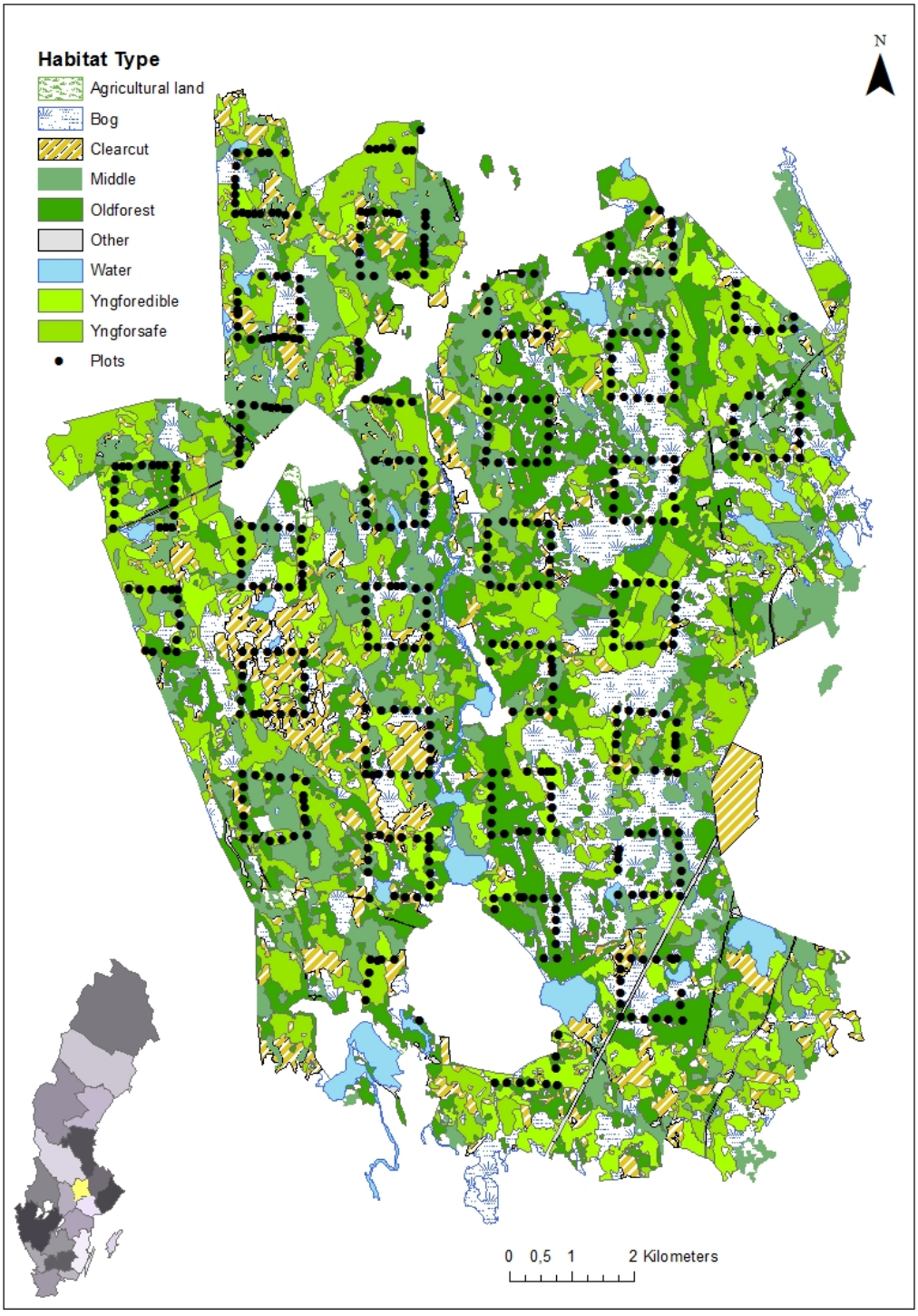

Figure 1 The location of the Grimsö Wildlife Research Area within Sweden (Västmanland county shown in yellow) and the distribution and position of the squares and plots within the research area used for data collection of moose pellet groups and pine consumption during 1996—2018. Map shows the forestry stand age based on 2016 data (Sveaskog GIS data).

Data Collection

Long term annual monitoring of the moose population and browsing pressure (proportion of twigs browsed during the previous winter) on tree species within permanent plots of 100 m^2 (5.64 m radius) has occurred since 1996. The plots are arranged within 32 1x1 km^2 squares systematically placed across the research area (figure 1). Except for the initial year 1996 (552 plots), 596 plots were surveyed annually from 1997-2016. Each plot in a particular square is 200 meters from the next plot so that there are five plots per side of a square and 20 plots per square (figure 2). As a result of small gravel roads and water bodies some squares have a total of less than 20 plots (Månsson *et al*, 2011).

I have conducted my study based on a before and after design. All years before wolves arrived back to Grimsö (n=7) are given a code of 0 and all years since wolves returned (n=13) are given a code of 1. A scent marking wolf pair was first discovered in the area in 2003/2004 (Wabakken *et* al, 2004), and my study states wolf presence begins in 2004 as the pellet counts will reflect the previous years moose density and subsequent moose habitat selection.

Moose pellet groups are counted within the plots as a measure of moose density and distribution, with a minimum of 10 single pellets required for the pellet group to be counted. The plots are cleared of old pellets in autumn (September-October) and surveyed in spring (April-May) with a mean accumulation period of 186 days (Månsson *et* al, 2011). Counts in spring represent the moose population from the preceding winter.

In addition to pellet counts the plots are also used to collect data on the amount of annual browsing pressure made to tree species in the plot through herbivory. The plot size for browsing data collection is 20m^2 (radius of 2.52m) but shares the same centre as the larger plot used for moose pellet counts. Browsing pressure is recorded on all trees between 0.3m and 3m in height as a proportion, i.e. the total number of shoots browsed is divided by the total number of shoots available (Månsson, 2009).

Every five years a more detailed census is made and the amount of available forage is also estimated for each plot. The forage estimate occurs within the 20m^2 plot and is only estimated if the tree is within moose browsing height of 0.3 - 3 meters (Månsson, 2009). The total estimated coverage (%) of the plot was recorded for aspen, downy birch, silver birch, rowan, juniper, willows and scots pine and spruce (Hörnberg, 2001). Summing all species forage estimates together for the plot can therefore tally up to more than 100%. (Månsson, 2009).

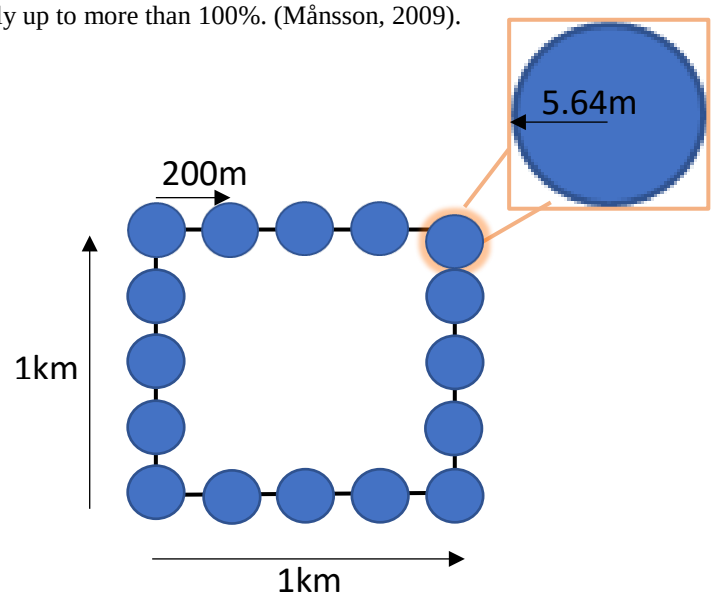

Figure 2 The design of the 1x1 km^2 squares showing each individual plot (radius of 5.64m), which are used for the annual survey of moose pellet and pine consumption in the Grimsö research area.

Response variables

I conducted my analysis based on indices of moose habitat selection to test my two predictions. Simple detection of moose pellets does not specify how the habitat was used and so I tested both the presence of moose pellet groups and pine consumption as two independent response variables. Finding pellets shows that moose have been in an area and can be used as a proxy for the time spent there. The more pellets found the more time moose are within those habitats. Moose tend to select conifer covered areas to rest (Belovsky, 1981). It is important to differentiate between when moose are simply resting versus feeding so I also used moose consumption of pine in my analysis to focus specifically on feeding behaviour in certain habitats.

I converted the moose pellet group counts into presence (1's) and absence (0's) and used data from 1997 to 2016. The first year of survey, 1996, was omitted as the pellet count was not conducted on cleared plots. The total sample size for the moose pellet group data was n = 11,020. All zeros in the data set were considered true 0's for moose absence.

The response variable describing consumption involved first taking the recorded browsing percentage for each plot and multiplying it by the amount of estimated available forage of pine for that plot (Bergström *et al*, 1995 IN Månsson, 2009). As browsing was only recorded when present it was not possible to know when browsing did not occur due to no forage being available, or due to no browsing taking place. By creating the consumption index, I could account for used pine forage versus available pine forage. Similar to the presence/absence of moose based on pellet groups I took the calculated consumption index and converted it into 1's and 0's. A lot of plots had no forage available and so the sample size for the consumption analysis was n = 4,649.

Explanatory variables

To explain the selection of habitat by moose I gathered multiple independent parameters based on the ecological literature of what governs moose habitat selection; Snow cover >10cm, distance to roads, distance to habitat classified as open/closed and dense, pine forage availability, deciduous forage availability and spruce cover availability. Wolf presence or absence was recorded for each year as was the average moose density.

Wolf Presence

Wolf occupancy and abundance in the area was based on annual monitoring from snow-tracking, radio-telemetry and DNA analysis conducted from October to February and presented in annual reports financed by the Norwegian Institute for Nature Research (NINA) and the Swedish Environmental Protection Agency (SEPA), (Wabakken *et al*, 2004).

Habitat

The Sveaskog company provided a GIS database of information on each stands age, productivity, management implementations as well as the location of bog habitat. I was able to use a 2016 dataset from Sveaskog for my analysis. I did not have comparable forestry-based data for privately-owned land and so I had to exclude plots

from the analysis that were not on Sveaskog land (n= 45). This reduced my annual sample size from n= 596 to n= 551 plots.

I decided to categorise habitat using forest stand age as age has been used in previous literature to define habitat types in connection to moose (Månsson *et al*, 2011). I divided forest stands into five stages of succession and had a sixth class designated as 'bog' habitat. At a forest stand age of 0 to 5 years I called the stand a clear-cut based on the CORINE land cover description of clear-cuts (Kosztra *et al*, 2017). Ages 6 to 15 years were considered a young dense forest with most trees within browsing reach of moose. Ages 16 to 35 represented a young dense forest of which most has grown outside the browsing height of moose. The young dense stages are based on Månsson (2009) who classified young forest as ages <30. In this study I have split the young stages up into an edible stage and a dense cover stage to portray the growth of the forest at a finer scale. Stands between 36 and 50 years were considered middle aged and older than 50 the forest was considered old forest.

To account for the dynamic nature of the forest as a result of the active management in the landscape I subtracted 1 from the age of each forest stand sequentially from 2016 to 1996. Each year in my final dataset therefore reflected what the forest stand ages were for that particular year of data collection. The next step was to categorise the ages of each stand into young, middle and old ages.

To test my primary hypothesis that wolves will reduce the time moose spend in open habitats I combined my forest categories into three classes. A 'dense' class consisted of all the young forest age 6 to 35 years, the 'closed' class represented all other forested habitat (ages 36 to >50) which will provide very little forage but could provide a visual cover from predators. Finally, I created an 'open' class which was clear cuts and bogs combined as I assume these two habitat types are mainly open (with no canopy).

I also examined the distance from each plot to the open, closed and dense classes in relation to wolf colonisation. I utilized the *NEAR* tool in ARC Map 10.5 to calculate the distance in meters from each plot to each of the three habitat classes.

Pine forage availability is thought to be higher in young dense stands (Bergström and Hjeljord, 1987 IN Månsson, 2009), heather is found mostly in bog habitat and bilberry is most available in older forests (Månsson, 2009). To test the robustness of my habitat categories I plotted pine forage, heather availability and bilberry availability, as well as moose pellets against my habitat classes. Appendix 1 shows that my habitat categories reflect the expected forage availability from the scientific literature.

Snow cover

To account for annual variation in snow depth I gathered data from the Swedish Meteorological and Hydrological Institute (SMHI[4]) on the number of days with more than 10cm of snow cover between November and April each year. To correct for different measurement efforts across months and years I took the number of snow days >10cm and divided it by the total number of winter days between November

[4] *https://opendata-download-metobs.smhi.se/explore/*

and April that the weather station recorded. The result was a proportion of snow days >10cm, which I used as explanatory variable. Data was taken from weather stations within 70 km of Grimsö (Kloten N°59.87 E°15.25, Ön N°59.40 E°15.1946, Grythyttan N59.71 E14.5301 and Västvalla N°59.42 E°15.61) and the values were averaged.

Roads

To test if roads had an impact on moose I calculated distance in meters (using ARCMAP 10.5 and the *NEAR* tool) from each plot to two categories of roads; 1) larger gravel roads, mainly the road surrounding the Grimsö wildlife research area 2) smaller roads, such as smaller forest roads. I used Swedish road data (road data from Lantmäteriet.se- Terrängkartan, accessed from the GET service provided by SLU) to create the two categories.

Forage availability

To test for the impact of forage availability on both moose presence and browsing pressure on each plot I created forage availability variables. As forage availability was only recorded every fifth year (1996, 2001, 2006, 2011 and 2016) I created an estimate of forage for every other year using linear interpolation:

$$\mathrm{F(t-1)} = \mathrm{Ft} - \frac{\mathrm{F(t-5)} - \mathrm{Ft}}{(t-5) - t}$$

where t= year and F= forage estimate.

To reduce model complexity and correct for the low abundance of deciduous trees recorded in the plots I summed the estimated cover of deciduous species including rowan, aspen, salix (spp.) and birch (spp.) for each plot into a single variable representing deciduous forage availability. I kept spruce as an independent variable due to its potentially important role as cover (Dussault *et al*, 2005) and the fact that it is minimally consumed by moose (Kalén and Bergquist, 2004). I also kept pine forage as a single variable as this species comprise the primary food item for moose during winter (Cederlund *et al*, 1980 IN Danell *et al*, 1991, Shipley *et al*, 1998).

Statistical analysis

All statistical analysis was performed using R software (version 3.4.1). I utilised the *glmmADMB* package developed by Skaug *et al* (2014) to run my models. I compared models using the Akaike's Information Criterion (AIC), as it allows the selection of the most parsimonious model (Burnham and Anderson, 2002).

Resource Selection Functions

I used resource selection functions (RSF) with presence/absence of pellet groups and pine consumption as response variables. Manly *et al* (2002) state that RSFs can be used when a comparison of used (presence) versus available (absence) habitat patches is required. I treated my absence data as true absences but as I do not formally state the detectability of moose pellet groups within a plot my analysis is a relative probability of use by moose on the various areas available to moose (Pearce and Boyce, 2006). A true probability of resource use results in a resource selection probability function (RSPF) and involves knowing the detection probability of the response variable (Mitchell and Hebblewhite, 2012).

Boitani and Powell (2012) acknowledge the growing use of RSFs within the ecological study of species and their habitat preferences. A wide range of literature is available on RSFs, mostly performed on radio telemetry or GPS data of animal locations (Hebblewhite and Merrill, 2008), however pellet counts have also been used for the analysis (Skarin, 2009, Gervasi *et al*, 2013).

I completed the resource selection functions using a logistic linear regression formula:

$$Y = \beta 0 + \beta n * Xn + \epsilon$$

where Y is a binary response variable, β0 is the intercept (mean of Y) and βn ∗ Xn is the slope of parameter n for a given value of n. ϵ is the error within the model that is left unexplained by the parameters.

Mixed model theory

As my data is based on repeated surveys of the same plots each year (longitudinal data) I needed to account for the variation within each plot using a mixed model (Collett, 2002). The mixed model design uses the variation found within the stated random effects and produces a random intercept γ alongside the models' intercept $\beta 0$. In my model design I used *plot* as a random effect and nested it within the *square* which was an attempt to take account of the spatial autocorrelation possible as a result of the plots being arranged within squares (Bataineh *et al*, 2006).

Model selection

Following Zuur *et al* (2010) I tested the collinearity between my explanatory variables (appendix 2ai). I further checked correlation between explanatory variables by calculating the Variance Inflation Factor (VIF) of each parameter. Each parameter is tested against all others for correlation and a single figure is produced (table 1). If the figure is more than 10 there is severe multiple collinearity and Zuur *et al* (2010) recommend a value below 3.

Table 1 Variance Inflation Factor for each explanatory variable used to analyse both pellet group presence and pine consumption presence. Values under 3 are considered to be free of multiple collinearity issues (Zuur et al*, 2010) and safe to have together within a model.*

Parameter	VIF
Pine Forage	1.17
Deciduous Forage	1.15
Spruce Availability	1.17
Distance to Big roads	1.13
Distance to Small roads	1.12
Days with snow cover >10cm	1.05
Distance to closed habitat	1.05
Distance to dense habitats	1.34
Distance to open habitats	1.28

The residuals of the models where plotted against each explanatory variable to see if the relationship to environmental variables was linear (Zhang, 2016). I found that for my analysis of pellet presence the parameters *pine forage* and *deciduous forage* were not linear and so I also introduced a quadratic term in the analyses. The analysis of consumption had non-linearity in the *deciduous forage*, *distance to closed*, *snow cover* and *moose density* parameters and I added quadratic expressions to be able to fit linear models (appendix 2aii).

I first built a generalised linear model with no mixed effects using only my *distance to open* parameter and the interaction of *wolf presence*, for both response variables. I then reran the model with the plots nested within squares as a nested random effect (named the basic mixed model below) for both response variables. I plotted the observed data on moose presence and pine consumption (y axis) against the fitted probabilities of both the fixed and mixed models (x axis). I expected that as the probability of moose presence and pine consumption increases I will get more observed moose presence and pine consumption, denoted via a positive diagonal line (appendix 2aiii).

As the pellet presence mixed model was 1,169.63 AIC units lower than the fixed effect model and the pine consumption mixed model was 471.29 AIC units lower than the fixed effects model I continued my model building using the mixed effect design.

After deciding on the mixed effect design I drew a receiver operating curve (ROC, Metz, 1978) for the basic model design which incorporated only the *distance to open habitat* and a *wolf presence* interaction. I calculated the area under the curve (AUC) to see how well the model could predict moose presence (Cumming, 2000). An AUC of 0.5 means the model is equivalent to guessing moose presence/pine consumption. I completed an ROC for both the pellet presence and pine consumption analysis. I compared the AUC value of the basic model design against the full (saturated) model design and the selected best model. The basic pellet presence model had an AUC of 0.54 while the full and best model both had an AUC of 0.7. The basic pine consumption model had an AUC of 0.66 while the full and best model had an AUC of 0.76 (see appendix 2c). Therefore the more complicated models were better at describing pellet group and pine consumption presence.

I built the saturated model by first adding all *distance to habitat class* parameters and their interactions with *wolf presence* and then the factor including *habitat types*. I added the parameters I was not primarily interested in but that might be of importance, proportion of snow days >10cm, distance to roads and availability of pine, deciduous forage and spruce (table 2). The analysis of pine consumption did not include a *pine forage availability* parameter as it was used to build the consumption index.

Table 2. Parameters used (✓) in the full models for both the moose pellet group and pine consumption analysis. I performed backward stepwise elimination on these full models using AIC values to select the most parsimonious model.

Parameter	Pellet analysis	Consumption analysis
Distance to Open habitats*	✓	✓
Distance to Closed habitats*	✓	✓
Distance to Dense habitats *	✓	✓
Wolf Presence	✓	✓
Habitat Type *	✓	✓
Pine forage	✓	×
Deciduous forage	✓	✓
Spruce availability	✓	✓
Snow days >10cm	✓	✓
Distance to big roads	✓	✓
Distance to small roads	✓	✓
Moose density/square	×	✓

* is a parameter that had an interaction with Wolf Presence

I performed backwards stepwise elimination by checking the full model read out and deleting the variables which had the lowest z score and highest p value and rerunning the updated model. Once the AIC ceased to decrease I stopped deleting variables (appendix 2.b for deleted variables). If a coefficient had the lowest Z score but its interaction coefficient was not the lowest I kept it in the model until first the interaction was deleted and then the parameter by itself if it still had the lowest Z score. I treated interactions in this way as deleting parameters changed the other coefficients of the remaining parameters and the Z scores and P values. Once the AIC increased I selected the model with the lowest AIC value. I also ran a likelihood ratio goodness of fit test on all models to see if there was a significant difference in the deviance explained in each model. If this was not the case I selected the model with the lowest number of parameters to reduce model complexity.

To calculate the probability of moose pellet group presence and pine consumption presence (Tables 3 and 6) I back transformed the logit coefficients of the best model. The back-transformation involves adding each habitat type, separately for before and after wolf return, to all the continuous variable coefficients. Each continuous variable coefficient must first be multiplied by its mean value. The intercept of my models was the bog habitat before wolf return and so all other habitat types must be added against the reference intercept value of bog. The habitat values after wolves returned involved also adding all the wolf interaction values for the particular habitat type onto the previous before-wolf value. All habitats after wolf return must add the bog-wolf interaction value as well. The decision of habitat selection or avoidance was based on the observed chance of presence of moose pellet groups or pine consumption from the raw data. The chance of finding a pellet group in a plot, regardless of habitat was

20% and pine consumption presence was 16%. The values were based on the actual number of present pellet groups or pine consumption divided by the total sample size.

Model construction

Pellet presence model

I built the full mixed model and tested its residuals against the explanatory variables which showed curvature, and so I rebuilt the full model with the necessary quadratic expressions (appendix 2aii) and kept the model with the lowest AIC.

The AIC scores showed model 5 was the lowest. A likelihood ratio goodness of fit test showed no significant difference in deviance explained between model 5 and the model with the lowest number of parameters (model 7) (χ^2=5.36, D.F.= 2, p-value= 0.07). Therefore, I selected model 7 as my best model due to its reduced complexity (Appendix, table 10).

My final analysis involved taking my best model (model 7) and remove, first, all wolf interactions and evaluate the changes in AIC, and finally remove the *wolf presence* parameter completely with evaluation of the change in AIC. If wolf presence was not an important parameter in explaining moose presence I expected that the removal of the parameter should reduce the AIC as model complexity is removed but variance explained is not affected, whereas if the AIC increases then the parameter is important in explaining the moose presence.

Pine consumption presence model

The full model was run with the mixed effect design and explanatory variables tested against the residuals for patterns. The curvature seen in some parameters resulted in the use of quadratic expressions in the model reducing the AIC from 3,416 to 3,411. I completed the rest of analysis with the quadratic expressions.

To account for potential changes in moose density between the time periods with and without wolves I summed all pellet groups by each square (n=32) for each year. I added the parameter both as a fixed effect (AIC=3356) and then as a random effect (AIC=3373). As the AIC was lowest with moose density as a fixed effect I used this for backwards stepwise model selection. I added a quadratic term to the moose density variable to correct for curvature which decreased the AIC from 3356 to 3337. My full model incorporates the moose density variable with the quadratic correction. As moose density values were only available from 1997 my pine consumption analysis was therefore performed from 1997-2016.

I followed the same process of model selection for the moose consumption of pine as I did for the moose presence analysis (Appendix, table 11). A likelihood ratio test on the lowest AIC model (model 6) versus the model including the lowest number of predictor variables (model 7) showed no difference (χ^2= 2.54, D.F.= 1, p-value= 0.111) and so I selected model 7 as my best model (Appendix, table 12).

My final check again was to see if *wolf presence* and its interaction with other variables were important in my best model (model 7). For this I used AIC and a likelihood ratio goodness of fit test to check the changes in model parsimony and deviance explained.

Model Validation

To validate my models, I tested how well they predicted presence of moose pellet groups and pine consumption. I used a confusion matrix to compare my predicted presence and absence results against the observed data (Boyce *et al*, 2002). I calculated the error of the model by dividing the correctly predicted presence and absence values against the sample size. To test specifically for the error of absence and presence separately I divided the correctly predicted absence values by the total amount of predicted absence and observed absence values. I did the same to test for predicted presence error. I also partitioned the data into two sections, one with 80% of the data and the other with the remaining 20%, in a form of cross-validation (Fielding and Bell, 1997). I reran the best model and completed a confusion matrix again, testing for the error in the predicted versus observed values. If the error rates increased it would be a sign that the model is not good at predicting when given new data.

I also used the Hosmer-Lemeshow Goodness of fit test to statistically test the predicted values against the observed values (Hosmer and Lemeshow, 1980 IN Lemeshow and Hosmer, 1982). The test partitions the predicted and observed values into 10 groups. If there is a significant difference within the groups then the predicted values are significantly different to the observed values and the model is not predicting well against the data given.

Results

The number of moose pellet groups and pine consumption varied over time (figure 3) with the average number of pellet groups before wolf recolonization 0.36 (+/- 0.02 standard error (SE)) and after wolves returned was 0.39 (+/- 0.01SE), however this difference is not statistically significant (Wilcoxon test; w= 13,959,000, p-value= 0.1912).

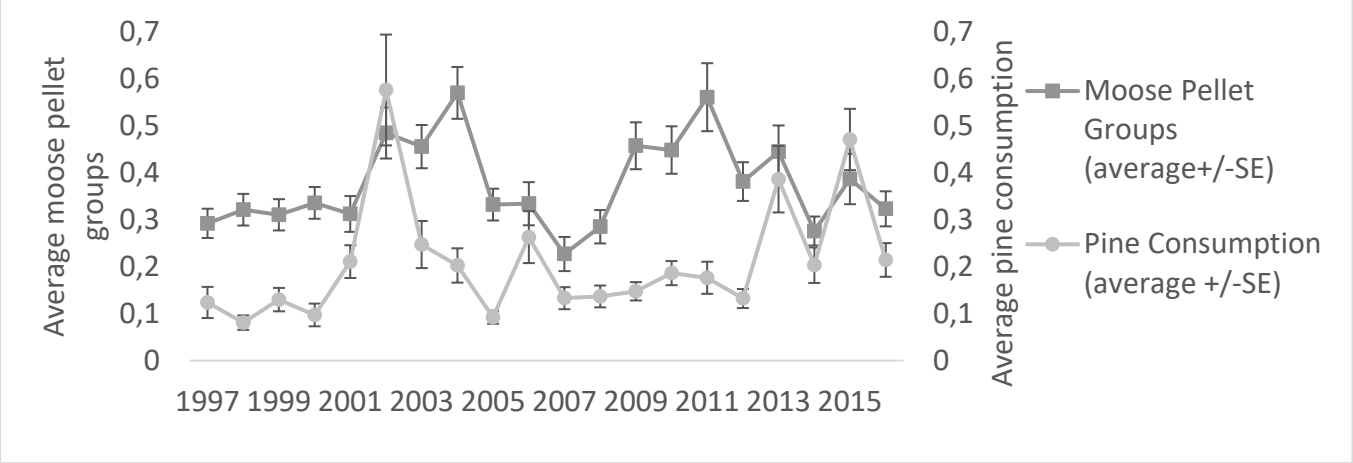

Figure 3. The annual variation seen in moose pellets and pine consumption found each year 1997-2016 at Grimsö Wildlife Research Area in Sweden. The years after 2004 represent the years when wolves had returned.

The average pine consumption before wolves returned was 0.20 (+-/ 0.04SE) and after wolves returned 0.21 (+-/ 0.04SE)

The average number of moose pellet groups within bogs was reduced, whereas the number in clear-cuts and middle-aged forest increased after wolf recolonization (figure 4). The amount of available pine forage before wolves returned was 4.12% (+/- 0.15SE) and 2.91% (+/- 0.08SE) after wolves returned.

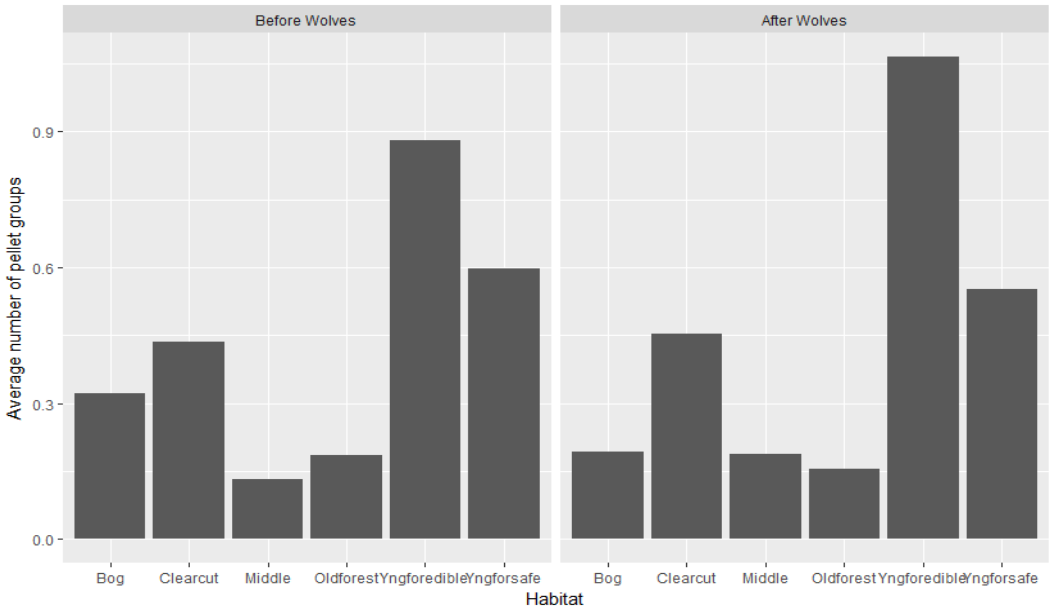

Figure 4. The distribution of observed moose pellets within each habitat class before (left panel) and after wolves returned (right panel).

The proportion of days with snow cover >10cm before wolves returned was 0.50 (+/- 0.002SE) and the years after wolves returned was 0.44 (+/- 0.003SE), indicating a significant difference between the two periods (Wilcoxon test; w= 15,787,000, p-value= <0.001- appendix 3).

The effect of wolf presence on moose pellet group distribution

Before wolves returned to the area moose neither selected nor avoided bog habitat (β= -1.38, 20% presence probability (pp), but avoided middle aged forest (β= -1.72, 15% pp) and old age forest (β= -1.54, 18% pp). Moose also actively selected for clear cuts (β= -1.075, 26% pp), young edible forest (β= -0.67, 34% pp) and young safe forest (β= -0.85, 30% pp). After wolves returned moose actively avoided bog habitat (β= -2.21, z-value= -4.47, p-value= <0.001, 10% pp), but significantly increased their selection of clear cuts (β= -0.81, z-value= 4.50, p-value= <0.001, 31% pp). After wolf colonisation moose continued to avoid middle aged forest (β= -1.53, z-value= 3.71, p-value= <0.001, 18% pp) and old age forest (β= -1.84, z-value= 2.86, p-value= 0.003, 14% pp). Moose presence decreased in young edible forest (β= -0.88, z-value= 2.57, p-value= 0.01, 29% pp) and in young safe forest (β= -1.15, z-value= 2.94, p-value= 0.003, 24% pp), (table 3, figure 5). There was no significant relationship between moose presence in different types of habitats and distance to cover in relation

to wolf presence as the distance parameters did not make it into the best model (table 4).

Table 3. The logits converted to probability of the habitat variables before and after wolf recolonization in the Grimsö Wildlife Research Area in south-central Sweden (1997-2016) and the corresponding probabilities of wolf presence. Logits 'after wolf' are the coefficient of the before wolf and after wolf for that particular habitat. The probability is calculated by $p = e^{yn} / (1 + e^{yn})$ *, where yn = the coefficient for a particular habitat type (6).*

	Coefficient logits (β)		**Presence probability (%)**	
Parameters	*Before Wolf*	*After Wolf*	*Before Wolf*	*After Wolf*
Bog	-1.376716	-2.207092	20	*9*
Clearcut	-1.074582	-0.8128448	26	*31*
YoungEdible	-0.6730398	-0.8784358	34	*29*
YoungSafe	-0.8541758	-1.150596	30	*24*
Middle	-1.719277	-1.52521	15	*18*
Old	-1.53939	-1.835658	18	*14*

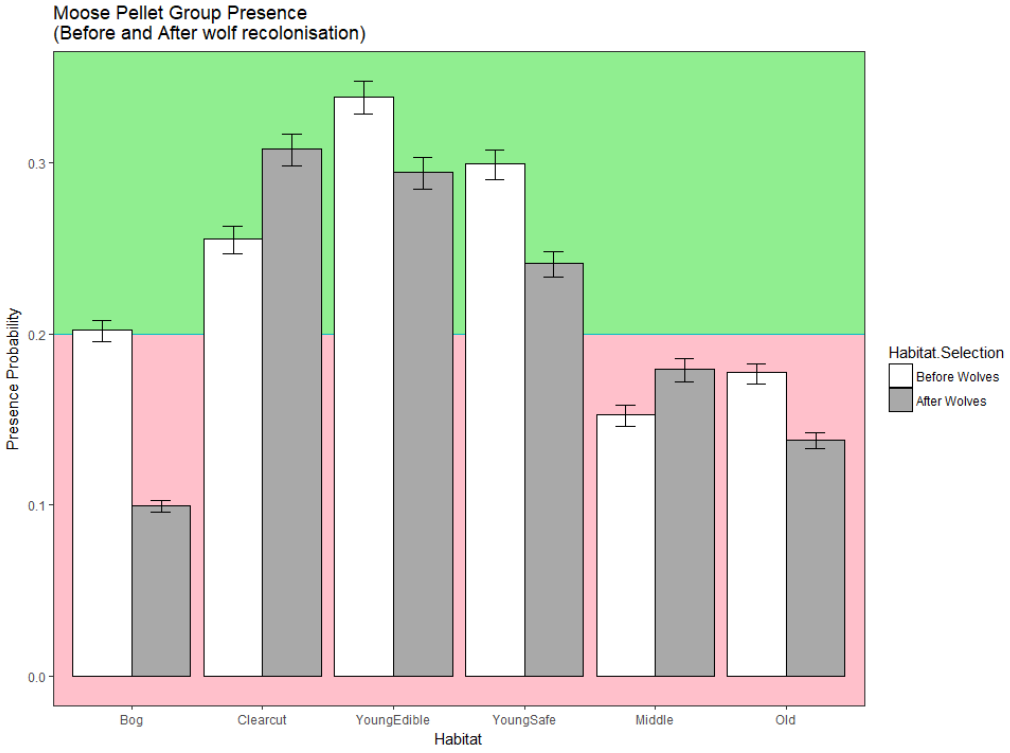

Figure 5. The back-transformed probability values for each habitat type from the analyses of the presence of moose pellet groups before and after wolves. Values within the green area means habitat selection whereas values within the red area means avoidance of a habitat type.

T*able 4. The distance to open, closed and dense parameters interaction with wolf presence, showing the lack of importance of wolf presence on how far moose where from different habitat types. Grimsö Research Area, 1997-2016*

Parameter	Coefficient (β)	Z-Value	P-Value
Distance to Open/Wolf Interaction	0.0007	0.99	0.32
Distance to Closed/Wolf Interaction	-0.00003	-0.02	0.98
Distance to Dense/Wolf Interaction	0.0007	1.16	0.25

There was a positive relationship between the probability of moose pellet group presence and proportion of days with snow depths >10cm (β= 0.90, z-value= 6.53, p-value= <0.001), pine forage (β= 0.10, z-value= 11.59, p-value= <0.001), deciduous forage (β= 0.05, z-value= 5.84, p-value= <0.001) and the distance to small roads (β= 0.001, z-value= 2.65, p-value= 0.008). Spruce availability was negatively related to the probability of presence of moose pellets (β= -0.01, z-value= -2.16, p-value= 0.031).

A likelihood ratio test showed that removing the interaction term of wolf presence from the habitat variable resulted in a poorer model (χ^2= 27.72, D.F.= 5, p-value= <0.001) and removing the wolf variable completely had a similar effect (χ^2= 29.52, D.F.= 6, p-value= <0.001). Therefore, the wolf parameter was an important variable within the best model and better explained moose pellet group presence.

Validation of the model (pellets)

Model results based on observed versus modelled moose absence and presence within a confusion matrix indicate that while the overall model predicts well (84%) this is largely due to the high number of areas correctly predicted as absent of moose (table 5). The ability of the model to predict moose presence is poor with an error of 20% as compared to 2% error in the detectability of moose absence. My other two validation techniques also showed the models were not good at predicting the presence of moose pellet groups (appendix 2c).

Table 5. Comparison of the observed moose presence and absence against the predicted presence and absence generated by the selected best model (MX7)

	Observed	*0*	*1*
Modelled	*0*	8619	1977
	1	183	241

The effect of wolf presence on moose pine consumption

Before wolves returned to the area the probability of moose pine consumption was highest in young safe forest followed by young edible forest, middle aged, old age, clear cuts and on bogs (table 6). After wolves returned pine consumption increased significantly on clear cuts (β= -2.28, z-value= 2.09, p-value= 0.036, 9% pp) and young edible forest (β= -0.96, z-value= 2.99, p-value= 0.003, 28%). No significant changes in consumption was found for bog (β= -3.40, z-value= -1.24, p-value= 0.213, 3% pp), middle aged forest (β= -1.94, z-value= 0.37, p-value= 0.714, 13% pp), old age forest (β= -2.91, z-value= 0.13, p-value= 0.899, 5% pp) or young safe forest (β= -1.58, z-value= 0.76, p-value= 0.448, 17% pp) (table 6/figure 9).

Table 6 The logits converted to probability. Each after-wolf logit is the added coefficient of after-wolf effect to the before-wolf coefficient for each habitat type. The probability of finding

pine consumption in each habitat class before and after wolf recolonization to Grimsö Wildlife Research Area

	Coefficient Logits (β)		**Consumption probability (%)**	
Parameters	*Before Wolf*	*After Wolf*	*Before Wolf*	*After Wolf*
Bog	-2.887115	-3.404115	5	3
Clearcut	-2.715115	-2.283115	6	9
YoungEdible	-1.497115	-0.9641148	18	28
YoungSafe	-1.297115	-1.575115	22	17
Middle	-1.727115	-1.943115	15	13
Old	-2.44115	-2.911615	8	5

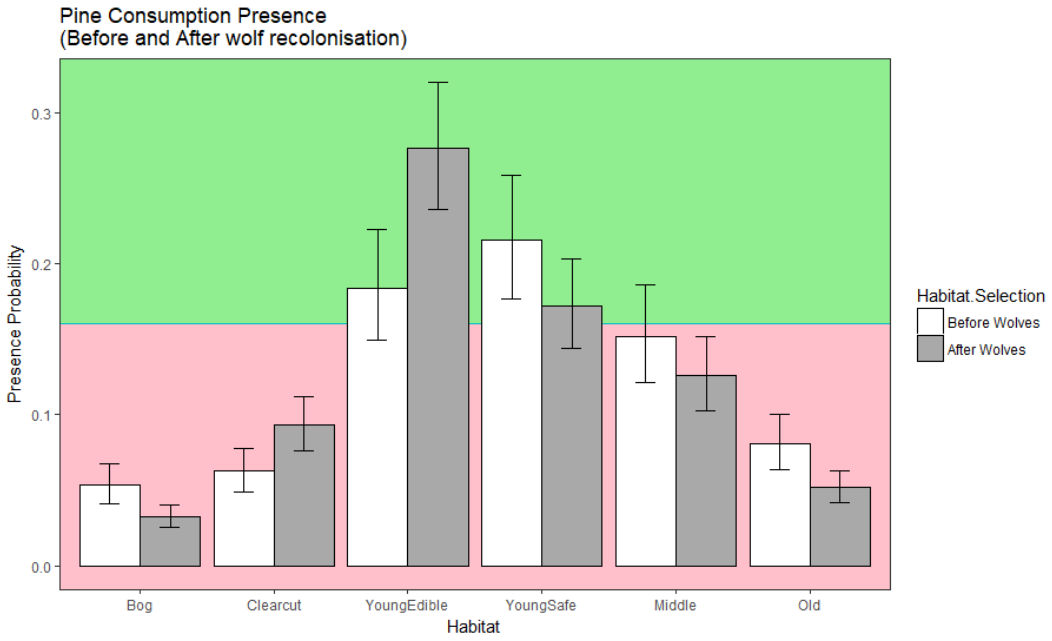

Figure 6. The coefficients of the consumption presence analysis for each habitat type before and after wolves in the Grimsö Research Area 1997-2016. Values within the green area represent habitat selection and values within the red area represent habitat avoidance.

The model also showed that as the distance from closed cover (middle aged and old age forest) increased, the probability of consumption on pine also significantly increased (0.007, z-value= 2.25, p-value= 0.024) (figure 7).

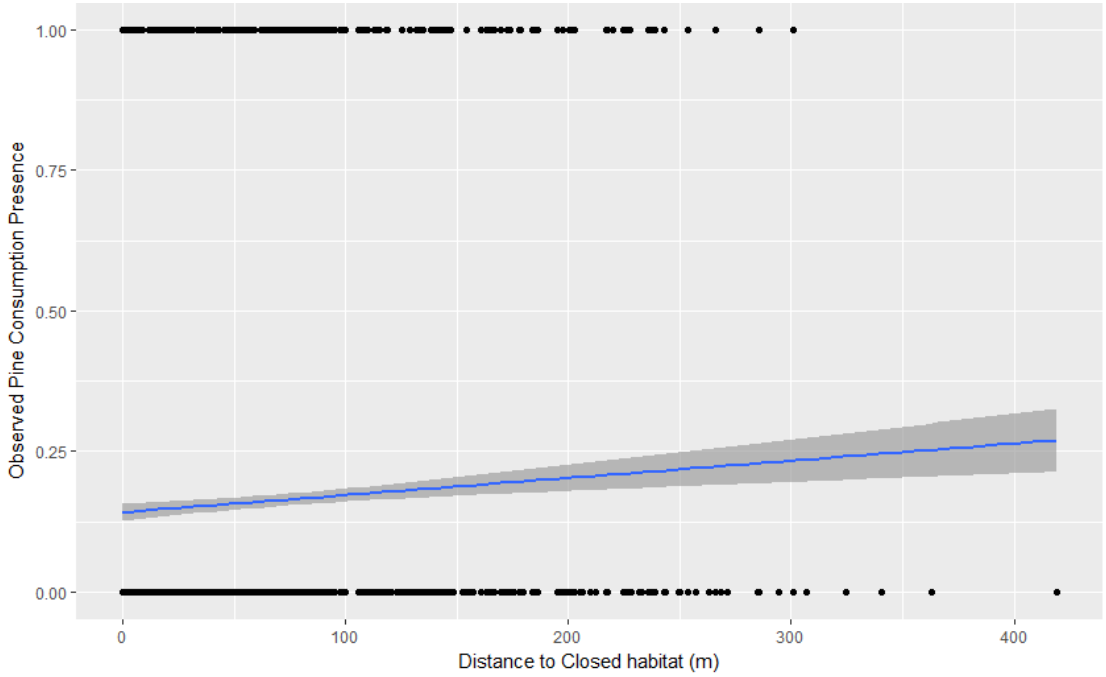

Figure 7. The predicted effect of how consumption is affected by distance to closed habitat, a significant increase in pine consumption occurs with increasing distance away from closed habitats.

However, the distance to dense habitat and open habitat types were not significant in the full model (table 7). Nor were the distance variables alongside an interaction term with wolf presence present in the best model.

Table 7. The distance to open, closed and dense habitat parameters interaction with wolf presence

Parameter	**Coefficient (β)**	**Z-Value**	**P-Value**
Distance to Open/Wolf Interaction	0.002	1.13	0.26
Distance to Closed/Wolf Interaction	0.0007	0.38	0.70
Distance to Dense/Wolf Interaction	0.00001	0.02	0.99

There was a positive relationship between moose consumption on pine and the four explanatory variables; proportion of snow cover days >10cm (β= 0.495, z-value= 2.02, p-value= 0.043), the distance to small roads (β= 0.001, z-value= 3.16, p-value= 0.002), the amount of deciduous forage (β= 0.05, z-value= 3.71, p-value= <0.001) and moose density (β= 0.176, z-value= 6.68, p-value= <0.001).

Removing the interaction term of wolf presence with habitat resulted in the model becoming significantly worse (χ^2= 13.2, D.F.= 5, p-value= 0.0216) as did removing the wolf parameter completely (χ^2= 14.08, D.F.= 6, p-value= 0.029). The best model to explain pine consumption therefore included the wolf presence variable.

Validation of the model (consumption)
The overall model had a good ability to predict moose consumption of pine (84%). However, the low error rate was mainly due to the correct prediction of consumption absence as seen in the confusion matrix (table 8). The model was not good at predicting the presence of pine consumption, with an error of 7.9%.

Table 8. The modelled presence and absence of consumption on pine versus the observed data. Grimsö Research Area, 1997-2016

	Observed	*0*	*1*
Modelled	*0*	3854	699
	1	41	55

My other two model validation techniques also showed the model was poor when predicting moose consumption of pine (appendix 2c).

Discussion

I predicted that after wolves returned to Grimsö Wildlife Research Area moose would show a higher selection for more closed habitats, avoiding bogs and clear cuts, and would feed at shorter distances from cover. In line with my hypothesis I found a significant reduction of time spent (pellet presence) by moose in bogs after wolves returned. However, I also found that the presence of moose significantly increased in clear-cuts after wolves returned as did the consumption of pine. Due to the discrepancy seen in moose selection of the two open habitat types, the hypothesis that moose will reduce time spent in open habitats after wolves return was not supported.

Open habitats, or forests in young successional stages, are believed to be risky environments as they have been shown to increase the chances of wolves successfully killing their prey (Kauffman *et al*, 2007, Gervasi *et al*, 2013). Moose have been shown to stay closer to more closed habitats when wolves are present, possibly due to the greater detectability wolves have of their prey in open habitats (Kunkel and Pletscher, 2000). My results show variability in moose winter habitat selection with greater avoidance of bogs after wolves returned but greater selection of clear-cuts. The lack of a measurable effect of wolves on the distance moose stay or feed from cover suggests wolf recolonization has not caused a behavioural change in moose habitat selection, even over a 13-year timeframe.

My results on moose habitat selection before wolves returned are similar to previous studies in areas without wolves. Moose did not select bogs as has been previously shown in Scandinavia (Ball *et al*, 2001, Cederlund and Okarma, 1988), and moose avoided middle-aged and older forest, a result similar to a previous study in the same area (Nicholson *et* al 2014). In winter the young dense forest stands are the preferred habitat for moose (Ball *et al*, 2001) which my results also supported. Moose mostly

use clear-cuts during the summer months (Pierce and Peek, 1984) and my analysis showed that moose, while not avoiding clear-cuts completely, did not select them as preferred feeding sites.

My study does however show a change in the habitat selection of moose since wolves returned, but the change witnessed does not follow my predictions. The results are not strong enough to say indirect effects of predation have caused the change. High moose mortality caused by human hunting is often given as an explanation for not finding the effects of wolves on their prey in Scandinavia as hunting accounts for >90% of moose mortality (Cederlund and Sand, 1991 IN Sand *et al,* 2006). It has been suggested that moose may have lost their anti-predator behaviour during the time wolves were absent and have not re-developed a sense of fear for wolves yet (Sand *et* al, 2006), or that moose have altered their antipredator strategy more towards human hunting methods (Ericsson, *et al,* 2015). Further, it is apparent that the effect of wolves depends on their proximity to the prey. Proffitt *et al* (2009) showed that although elk stayed close to cover when wolves were present, if wolves were more than 5 kilometres from the elk then they did not show a changed browsing pattern. In Scandinavia the high moose to wolf ratio results in individual moose having a low encounter probability with wolves (Eriksen *et al,* 2009). Wikenros *et al* (2016) showed that the distance between a moose and a wolf in the Grimsö Wildlife Research Area was on average 11 km, and could explain why I found no effect of distance from cover before and after wolf recolonization.

It is more likely that my results reflect a functional response of moose to forage availability. The most striking change is the reduction in pellet group presence in the preferred moose habitat of young edible forest but at the same time an increased pine consumption presence. I show that as pine and deciduous forage increased in availability so did the chances of finding both pellet groups and pine consumption. During winter moose select areas which have a large quantity of forage over areas with high quality forage in an attempt to maximise energy intake (Van Beest *et al,* 2010). It has been shown that as the relative availability of a particular habitat type increases moose will reduce their selection for it (Herfinal *et al*¸2009) and that with increasing density of saplings, browsing is directed less towards individual saplings and more towards covering a greater amount of area in the forest stand (Vivås and Saether, 1987). The reduction in pellets within young dense edible forest as well as a significant increase in the presence of pine consumption is explainable from the functional response theory. The years after wolf recolonization showed an increase in the availability of young edible forest stands (Appendix 4) which would cause a reduction in pellet group presence as more habitat is available for the moose, but they will cover a greater amount of area and so increase the presence of pine consumption.

My discovery that moose now select clear-cuts significantly more is an interesting result. The increased selection of clear-cuts by moose after wolves returned was contrary to what I predicted. Moose try to avoid overly dense forest stands until the winter becomes too severe (Peek *et* al, 1976) and then moose begin to select more dense cover as forage from the field layer gets covered with snow and conditions drive moose to seek shelter and food within denser forests (Pierce and Peek, 1984, Månsson, 2009). A lack of selection of clear-cuts before wolves returned is possibly linked to an artefact of hard winters forcing moose to move into the dense forest

stands. My data show a significantly higher proportion of snow days >10cm before wolves returned and the increased selection of clear-cuts after wolves returned could be due to moose delaying the decision to move into the dense forests. Vivås and Saether (1987) state that the decision to leave a feeding patch should occur when the rate of food intake becomes lower than the average rate of intake. If the field layer and young trees are available for a relatively longer time period during the year, due to reduced number of days with snow, then moose will possibly stay out in the clear-cuts for longer.

If wolves are having an effect on moose it is not causing them to avoid a previously used habitat. Fortin *et al* (2005) show that elk do not avoid moving through core wolf use areas but do change their habitat use when moving in the high-risk environment. So, it is possible that my finding of a change in the proportional use of habitat types since wolves returned is linked to predation fear, however any such effect is occurring at an extremely fine scale, as already indicated by Nicholson *et al* (2014). The inclusion of interaction terms with the wolf presence variable made the models significantly better, however my results are blurred by the confounding effects of climate and the fluctuating effects of resource availability.

A problem with RSFs is poor model fit due to fluctuations in resource availability (Boyce *et al*, 2002). I used a varying habitat variable to account for the dynamic nature of forest succession due to forestry management actions. I attempted to control for the potential pitfall of changes in resource availability by adding random effect components to my model. I followed Hebblewhite and Merrill (2008) in creating a mixed effect model to correct for changes in covariates for each plot, much like they did for each individual wolf. The method has been used by Gillies *et al* (2006) to accomplish the same goal. As well as variable resource availability, figure 3 shows that the latter years of Grimsö research area possibly had higher moose numbers, however the medians of the two periods are not significantly different.

My model diagnostics showed a low ability to predict the presence of moose pellet groups and pine consumption presence. Boyce *et al* (2002) felt AUC values over 0.7 indicated the model is a satisfactory fit of the data, and my best models had AUC values of 0.7 or higher. My models correctly predicted moose winter habitat selection as based on previous research which gives them a level of reliability.

The positive effect wolves have been shown to have on vegetation recovery in North American systems have promoted the idea that ecosystems can be restored by reintroducing previously exterminated apex predators (Manning *et* al, 2009) and that forestry damages could be reduced if predators are present (Bojarska *et al*, 2017, van Ginkel *et al*, 2018). The complexity of anthropogenic influence within many European studies has made it difficult to generalise the effects a predator will cause to its prey (Kuijper *et al*, 2016). In this study I complement previous research results that wolves have not caused a change in moose behaviour in Sweden. I have uncovered a change in habitat selection between two time periods which reinforces the difficulties of exploring data in a before and after framework. The fact that a change has been seen after wolves return warrants further investigation to see if the intricate details of moose habitat use can be untangled. An important aspect of the results is the increased level of pine consumption within the young edible forest

stands. Forestry management must take account of the availability of forage for moose when deciding to cut down or alter forest stands in an area. If the balance in age categories changes so that there is an abundance of forage it could result in increased browsing across greater areas of vulnerable young forest stands. At the moment it remains that moose in Sweden have not felt the fear of the wolf.

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Appendix

1. *Habitat Categorisation*

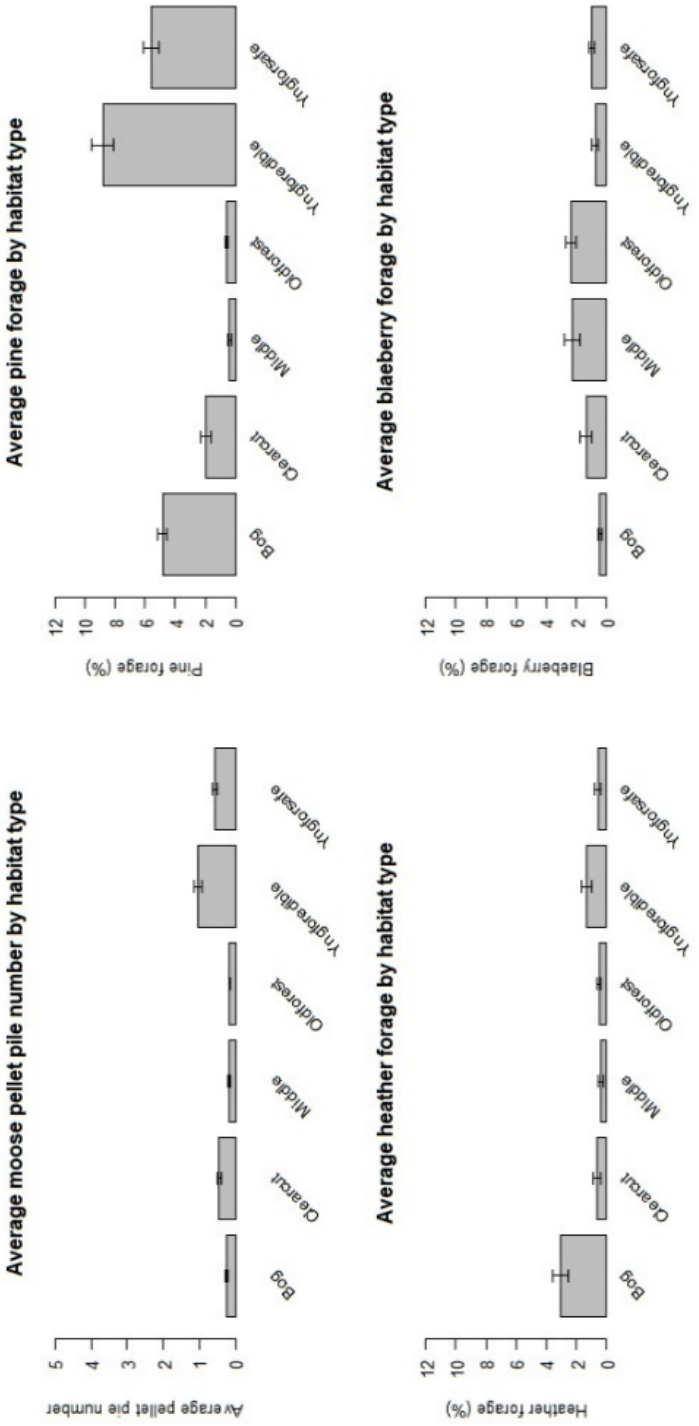

Figure 8 Testing my habitat classifications against availability of forage of pine, heather and blueberry to see if the observed matched the expectations. Error bars represent standard error (95% confidence limit)

2. *Analysis*

a. *Model Preparation*

i. *Correlation of variables*

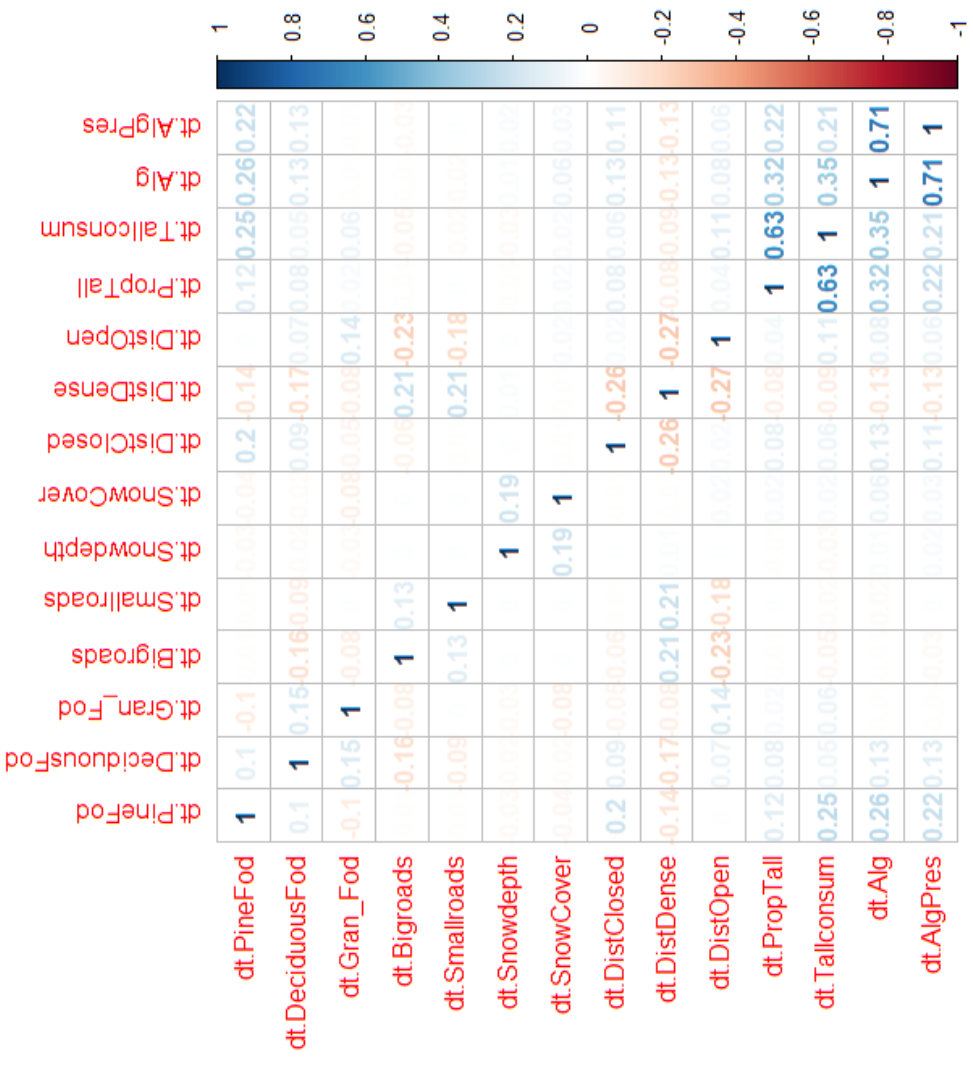

Figure 10. The correlation between the different explanatory variables used within the logistic regression models

ii. Linearity of explanatory variables

Moose Pellet Presence analysis

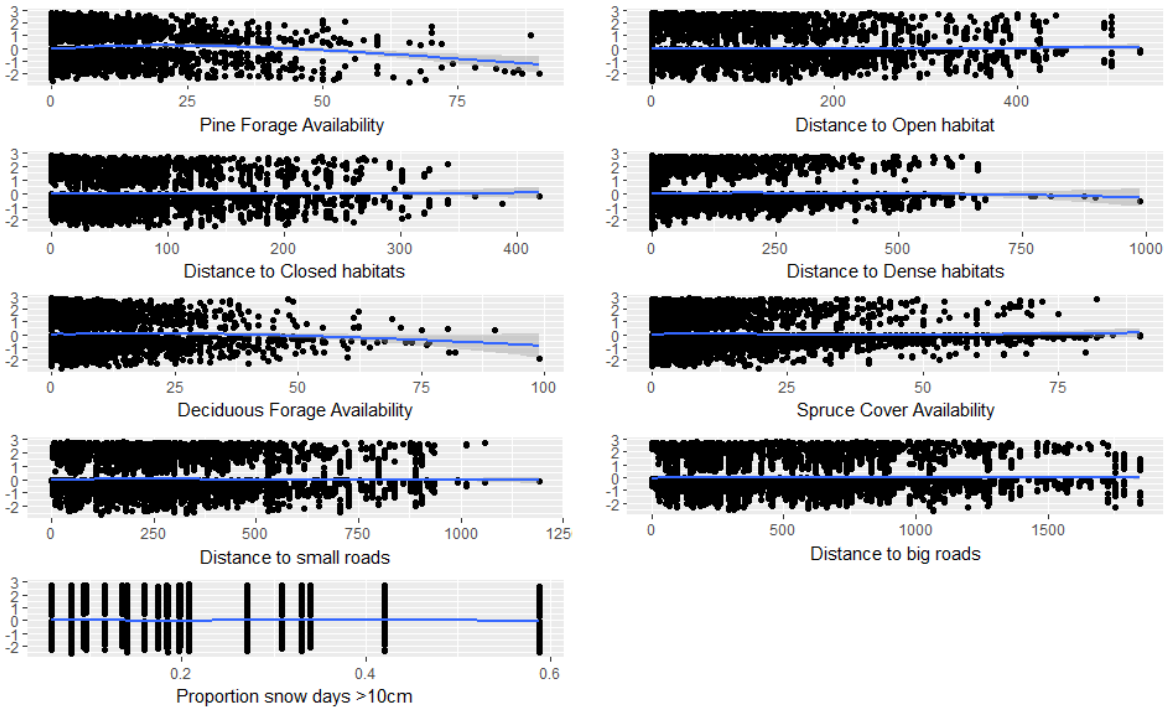

Figure 10. The linearity of explanatory variables using the standardised residuals from the full model. Pine Forage availability and Deciduous forage availability show a curved line.

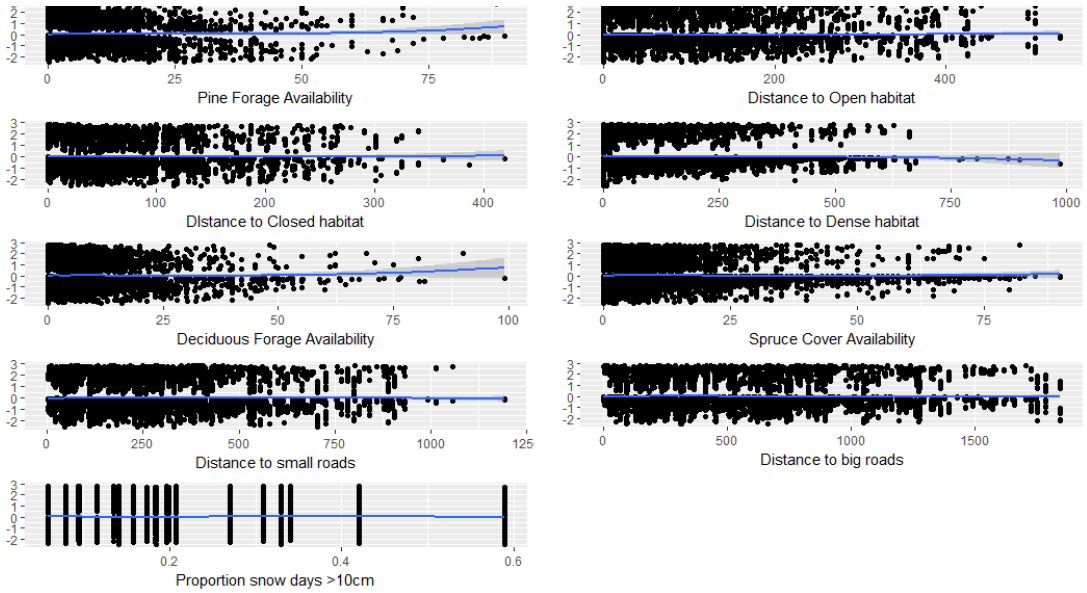

Figure 11. After adding a quadratic expression to Pine forage and deciduous forage availability the standardised residuals are more linear.

Pine Consumption analysis

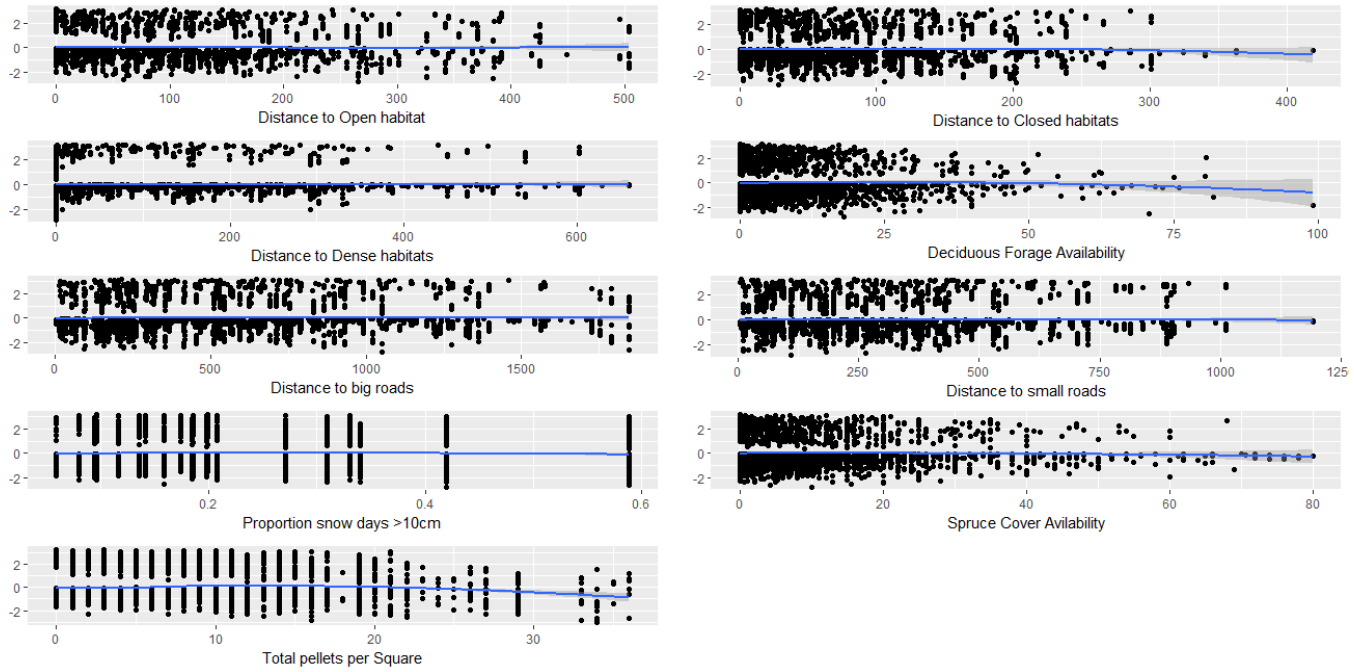

Figure 12. The explanatory variables used in the pine consumption analysis.

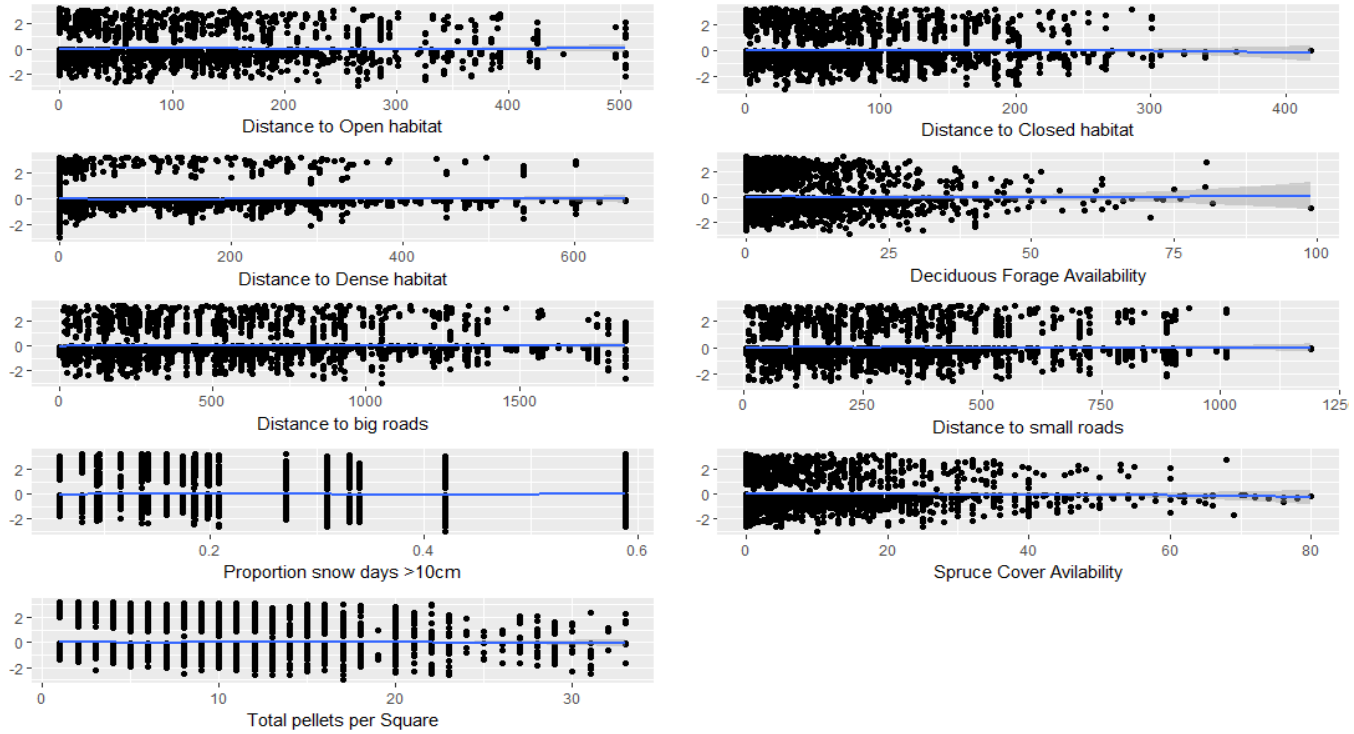

Figure 13. A quadratic expression was added to Deciduous forage availability and Total pellets per Square (moose density estimate). The explanatory variables are now more linear

iii. GLM vs GLMM

Pellet Presence

Plotting the probability of moose presence against the observed moose presence for both the fixed effect and mixed effect models containing only *distance to open habitat* and an interaction with *wolf presence.* It is clear that the mixed effect model better reflects the expectation that as the probability of presence increase so to does the observed moose presence (blue line – figure 14).

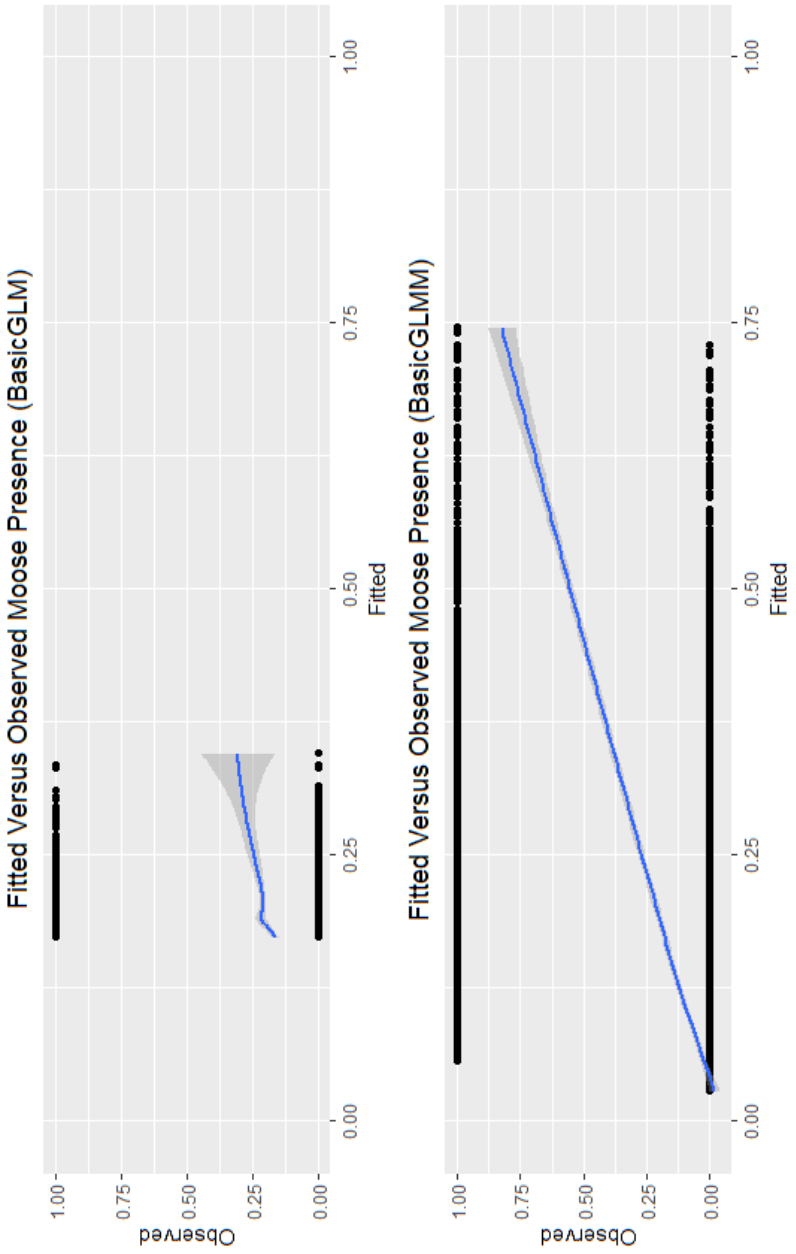

Figure 14. The fitted probabilities against observed moose presence of the basic fixed effect model versus the basic mixed effect model. Both graphs only show the smoothed loess line for easy comparison.

Pine consumption

Plotting the probability of pine consumption against the observed pine consumption for the fixed effect and mixed effect models containing only *distance to open habitat* and an interaction with *wolf presence.* It is clear that the mixed effect model better reflects the expectation that as the probability of presence increase so to does the observed moose presence (blue line – figure 15).

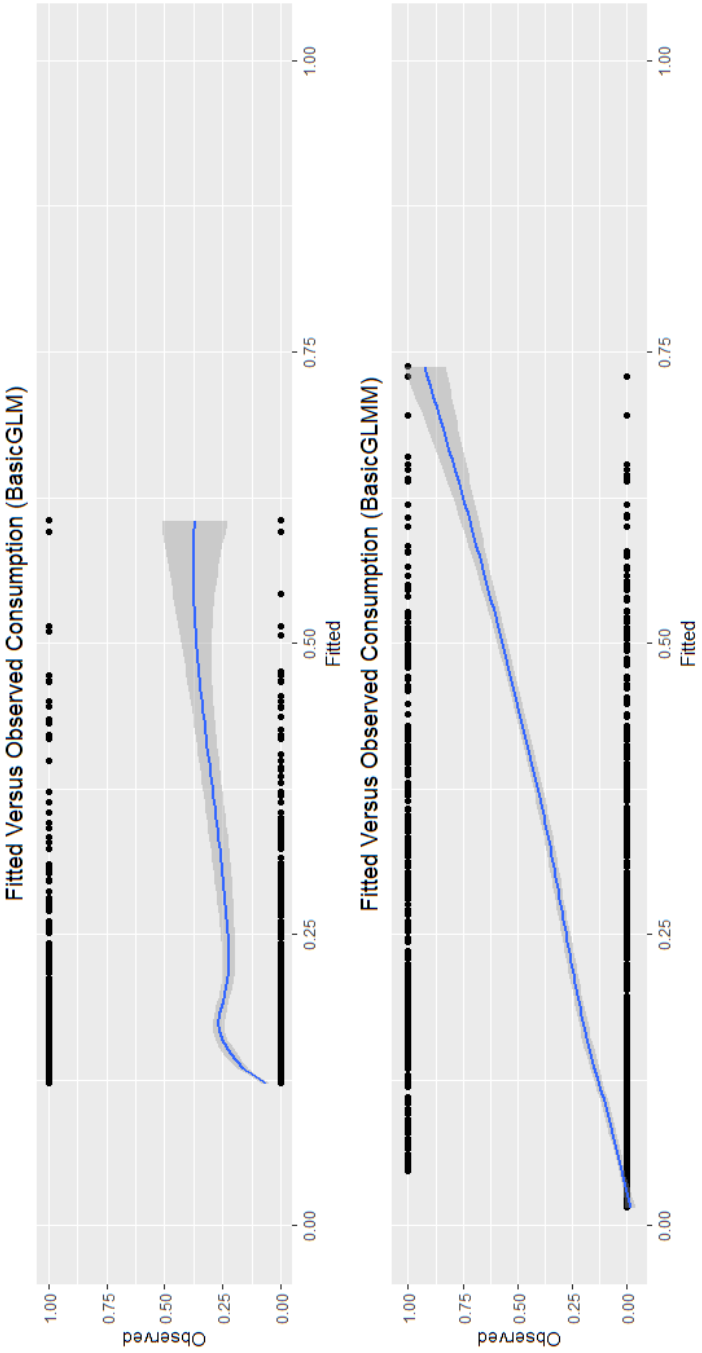

Figure 15. Fitted probabilities against the observed moose consumption on the fixed effect basic model versus the mixed effect basic model.

b. Model Selection

Backwards elimination- Pellet presence model

Table 9 The AIC scores for all models run within the Pellet group presence analysis. M7 was selected as the best model.

Model	Parameter included	AIC
FULL	Distance to Open*Wolf Presence Distance to Closed*Wolf Presence Distance to Dense*Wolf Presence Distance to Open Distance to Closed Distance to Dense Wolf Presence Habitat Type*Wolf Presence Habitat Type Pine Forage Deciduous Forage Spruce Availability Number of snow days >10cm Distance to big roads Distance to small roads	9333.5
M1	Distance to Open*Wolf Presence Distance to Dense*Wolf Presence Distance to Open Distance to Closed Distance to Dense Wolf Presence Habitat Type*Wolf Presence Habitat Type Pine Forage Deciduous Forage Spruce Availability Number of snow days >10cm Distance to big roads Distance to small roads	9331.5
M2	Distance to Open*Wolf Presence Distance to Dense*Wolf Presence Distance to Open Distance to Dense Wolf Presence Habitat Type*Wolf Presence Habitat Type Pine Forage	9330.64

	Deciduous Forage Spruce Availability Number of snow days >10cm Distance to big roads Distance to small roads	
M3	Distance to Dense*Wolf Presence Distance to Open Distance to Dense Wolf Presence Habitat Type*Wolf Presence Habitat Type Pine Forage Deciduous Forage Spruce Availability Number of snow days >10cm Distance to big roads Distance to small roads	9328.7
M4	Distance to Open Distance to Dense Wolf Presence Habitat Type*Wolf Presence Habitat Type Pine Forage Deciduous Forage Spruce Availability Number of snow days >10cm Distance to big roads Distance to small roads	9327.72
M5	Distance to Dense Wolf Presence Habitat Type*Wolf Presence Habitat Type Pine Forage Deciduous Forage Spruce Availability Number of snow days >10cm Distance to big roads Distance to small roads	9327.22
M6	Wolf Presence Habitat Type*Wolf Presence Habitat Type Pine Forage Deciduous Forage Spruce Availability	9327.34

	Number of snow days >10cm Distance to big roads Distance to small roads	
M7	Wolf Presence Habitat Type*Wolf Presence Habitat Type Pine Forage Deciduous Forage Spruce Availability Number of snow days >10cm Distance to small roads	9328.34

Selected best pellet group presence model output

Table 10. Output of pellet group presence model M7

Coefficients:	**Coefficient**	**Std. Error**	**Z value**	**P value**
Intercept (BOG)	-2.590392	0.20431	-12.68	< 2e-16
Wolf Presence (BOG)	-0.830376	0.14286	-5.81	6.20E-09
Clearcut	0.302134	0.22571	1.34	0.1807
Middle Aged Forest	-0.342561	0.28233	-1.21	0.225
Old Aged Forest	-0.162674	0.19229	-0.85	0.39756
Young Edible Forest	0.703676	0.23899	2.94	0.00324
Young Safe Forest	0.52254	0.19941	2.62	0.00878
Pine Forage	0.101361	0.008776	11.55	< 2e-16
Pine Forage (^2)	-0.001253	0.000176	-7.11	1.10E-12
Deciduous Forage	0.053453	0.009112	5.87	4.50E-09
Deciduous Forage (^2)	-0.000633	0.000174	-3.63	0.00029
Spruce Cover	-0.007428	0.003278	-2.27	0.02346
Proportion Snow cover >10cm	1.259582	0.23645	5.33	1.00E-07
Distance to small roads	0.000673	0.000256	2.63	0.00855
Wolf Presence (Clearcut)	1.092113	0.24125	4.53	6.00E-06
Wolf Presence (Middle Aged)	1.024443	0.28486	3.6	0.00032
Wolf Presence (Old Aged)	0.534108	0.1822	2.93	0.00337
Wolf Presence (Young edible)	0.62498	0.24027	2.6	0.00929
Wolf Presence (Young safe)	0.533956	0.18554	2.88	0.004

Backwards elimination- Pine consumption model

Table 11. The AIC scores for all models run within the Pine consumption presence analysis. M7 was selected as the best model.

Model	Parameter included	AIC
FULL	Distance to Open*Wolf Presence Distance to Closed*Wolf Presence Distance to Dense*Wolf Presence Distance to Open Distance to Closed Distance to Dense Wolf Presence Habitat Type*Wolf Presence Habitat Type Moose Density Deciduous Forage Spruce Availability Number of snow days >10cm Distance to big roads Distance to small roads	3332.28
M1	Distance to Open*Wolf Presence Distance to Closed*Wolf Presence Distance to Open Distance to Closed Distance to Dense Wolf Presence Habitat Type*Wolf Presence Habitat Type Moose Density Deciduous Forage Spruce Availability Number of snow days >10cm Distance to big roads Distance to small roads	3330.28
M2	Distance to Open*Wolf Presence Distance to Closed*Wolf Presence Distance to Open Distance to Closed Distance to Dense Wolf Presence Habitat Type*Wolf Presence Habitat Type	3328.28

	Moose Density Deciduous Forage Spruce Availability Number of snow days >10cm Distance to small roads	
M3	Distance to Open*Wolf Presence Distance to Open Distance to Closed Distance to Dense Wolf Presence Habitat Type*Wolf Presence Habitat Type Moose Density Deciduous Forage Spruce Availability Number of snow days >10cm Distance to small roads	3326.48
M4	Distance to Open Distance to Closed Distance to Dense Wolf Presence Habitat Type*Wolf Presence Habitat Type Moose Density Deciduous Forage Spruce Availability Number of snow days >10cm Distance to small roads	3325.96
M5	Distance to Open Distance to Closed Distance to Dense Wolf Presence Habitat Type*Wolf Presence Habitat Type Moose Density Deciduous Forage Number of snow days >10cm Distance to small roads	3325.52
M6	Distance to Open Distance to Closed Wolf Presence Habitat Type*Wolf Presence Habitat Type Moose Density	3325.02

	Deciduous Forage Number of snow days >10cm Distance to small roads	
M7	Distance to Closed Wolf Presence Habitat Type*Wolf Presence Habitat Type Moose Density Deciduous Forage Number of snow days >10cm Distance to small roads	3325.86

Selected best pine consumption presence model output

Table 12. Output of model M7 (Pine consumption Analysis)

Coefficients:	**Estimate**	**Std. Error**	**Z value**	**P value**
Intercept (BOG)	-5.5900	0.3910	-14.3000	< 2e-16
Moose Density	0.1740	0.0262	6.6400	0.0000
Moose Density (^2)	-0.0040	0.0009	-4.4300	0.0000
Wolf Presence (BOG)	-0.5170	0.2500	-2.0700	0.0383
Distance to closed habitat	0.0075	0.0033	2.2600	0.0240
Distance to closed habitat (^2)	0.0000	0.0000	-2.1000	0.0354
Clearcut	0.1720	0.3690	0.4700	0.6401
Middle Aged Forest	1.1600	0.7750	1.5000	0.1334
Old Aged Forest	0.4430	0.3790	1.1700	0.2427
Young Edible Forest	1.3900	0.3300	4.1900	0.0000
Young Safe Forest	1.5900	0.3040	5.2100	0.0000
Deciduous Forage	0.0510	0.0135	3.7700	0.0002
Deciduous Forage (^2)	-0.0004	0.0002	-1.7300	0.0832
Proportion Snow cover >10cm	3.6400	1.4500	2.5100	0.0122
Proportion Snow cover >10cm (^2)	-3.9100	2.2100	-1.7700	0.0774
Distance to small roads	0.0013	0.0004	3.1800	0.0015
Wolf Presence (Clearcut)	0.9490	0.4310	2.2000	0.0275
Wolf Presence (Middle Aged)	0.3010	0.8190	0.3700	0.7138
Wolf Presence (Old Aged)	0.0495	0.3920	0.1300	0.8994
Wolf Presence (Young edible)	1.0500	0.3410	3.0700	0.0022
Wolf Presence (Young safe)	0.2390	0.3150	0.7600	0.4482

Table 13. The means and range for the continuous variables found within the best models of the pellet group and pine consumption presence analysis. These figures can be used to back transform the model coefficients into probabilities of presence.

Parameter	Min	Max	Mean	BeforeMean	AfterMean
Pine Fod	0	90	3.33	4.12	2.91
Decid Fod	0	99	3.71	3.5	3.82
Spruce Fod	0	90	8.98	10.75	8.02
Snow	0.078	0.77	0.46	0.50	0.44
Small Roads	1.44	1191.31	298.49	298.49	298.49
PellTraktSum	0	36	6.9	6.59	7.07
MoosePellCount	0	20	0.38	0.36	0.39
DistClosed	0	419	44.5	44.82	44.41

c. *Model Validation*

Moose Pellet Presence

By partitioning my data into two parts, a training part consisting of 80% of my data and a validation set containing the remaining 20% I could test how well the model predicted the validation set of data. The selected model predicted both absence error (2%) and presence error (12.96%) which was similar to the full model. If the error rates had increased it would be a sign that the model is not good at predicting when given new data.

The poor ability of the model when predicting moose presence is shown when the modelled predictions for each plot are compared against the observed moose data for each plot. A Hosmer-Lemeshow Goodness of Fit test partitioned 10 groups of predicted versus observed moose presence showed significant differences between the predicted and observed groups (χ^2=78.93, D.F.=8, p-value= <0.001). A better performing model would not show a significant difference between the groups.

Pine Consumption

To complete the investigation of the model I again created a training and validation dataset. After running the model again on only 80% of the data and testing it against the remaining 20% the error rate for presence of consumption is similar (7.1%) to that ran on all the data. If the model was very poor then when it is tested on new data the error rate would be higher.

The Hosmer-Lemeshow Goodness of Ft test was performed on 10 groups of predicted versus observed presence of consumption and suggests that the model is not good at predicting (χ^2= 40.06, D.F.= 8, p-value= <0.001).

Pellet Presence ROC graph

The explanatory power of the model was tested first by drawing a Receiver Operating Curve (ROC) and checking the Area Under the Curve (AUC). Figure 16 shows the ROC and AUC for the basic mixed model, the full model and model 7. The basic model does not model the response variable well with an AUC value close to 0.5 and thus similar to guessing moose presence and absence. The full and best models both

have better AUC scores, and as model M7 was not significantly different than the full model (χ^2= 8.84, D.F.= 7, p-value= 0.264) it is the selected best model.

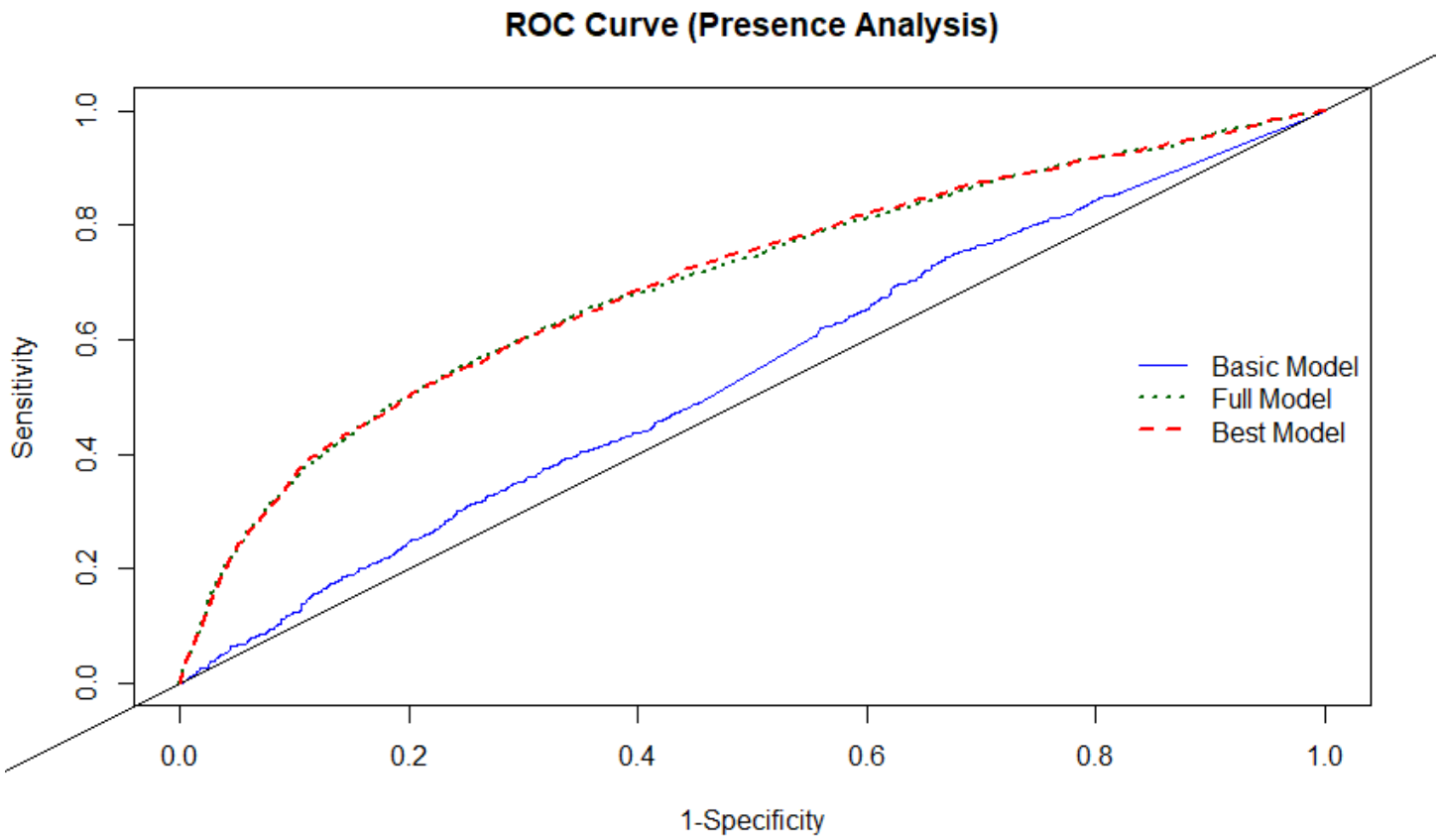

Figure 16. Receiver Operating Curve showing the basic mixed model (blue), full model (orange) and selected best model (red) ability to predict better than guess work (black line; 0.5). An AUC of 1 represents a perfect fit.

Pine consumption ROC graph

The Receiver Operating Curve (ROC) and Area Under the Curve (AUC) was plotted for the basic mixed model, full model and selected best model (figure 17).

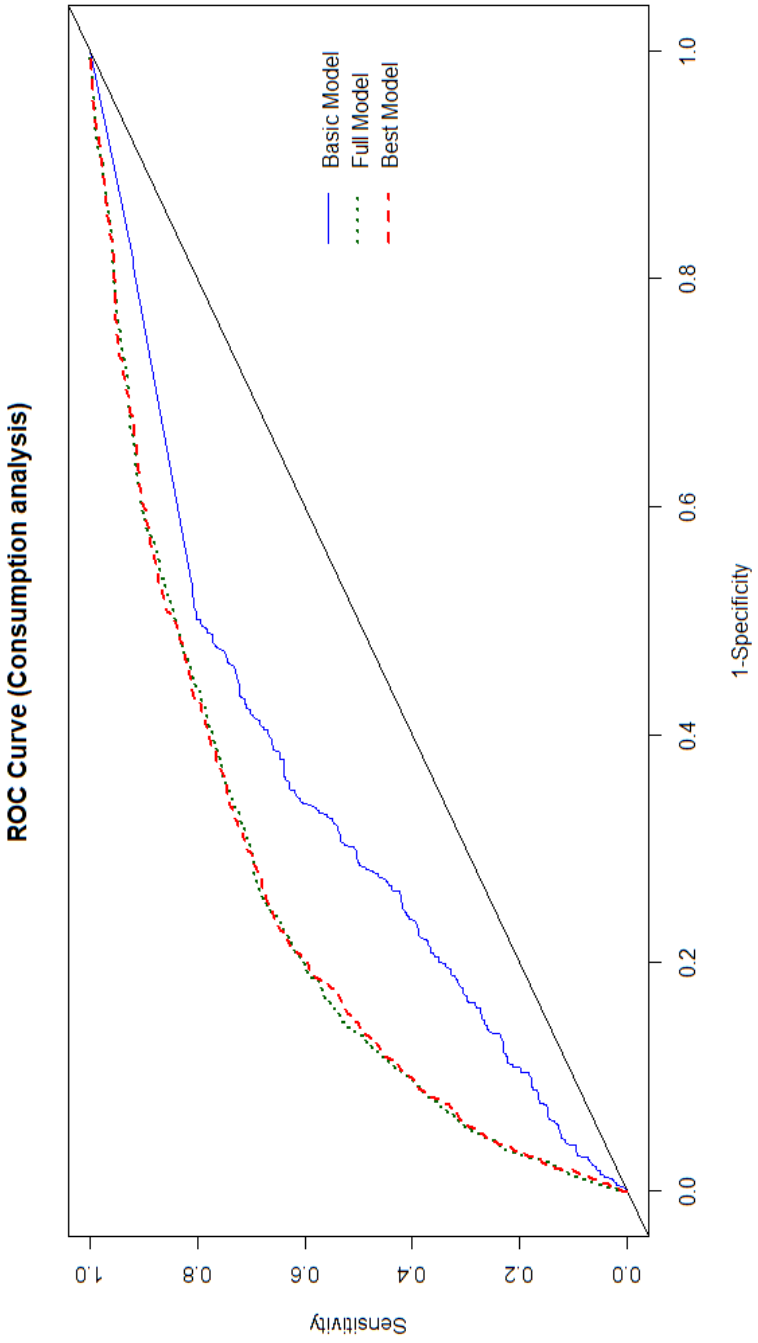

Figure 17.ROC and AUC for the basic (blue), full (green) and best (red) model, plotted against a predictor (black) line which represents a model that is correct 50% of the time.

3. *Continuous variables distribution before and after wolves*

Pine Forage

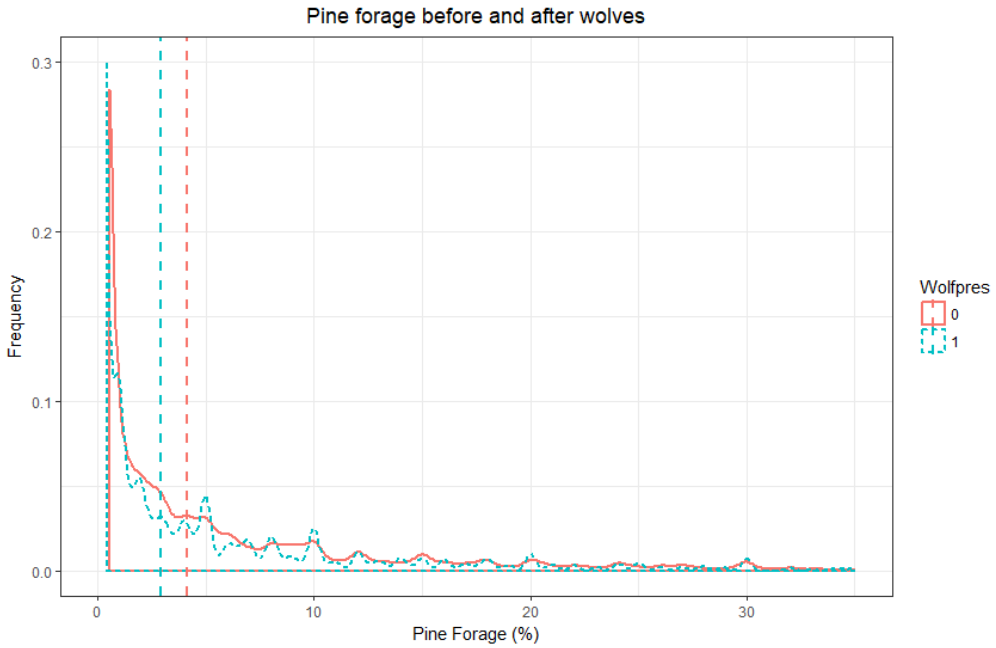

Figure 18. The distribution of pine forage before (red) and after (blue) wolf presence. Vertical dashed lines represent the average pine forage before and after wolf return

Deciduous Forage

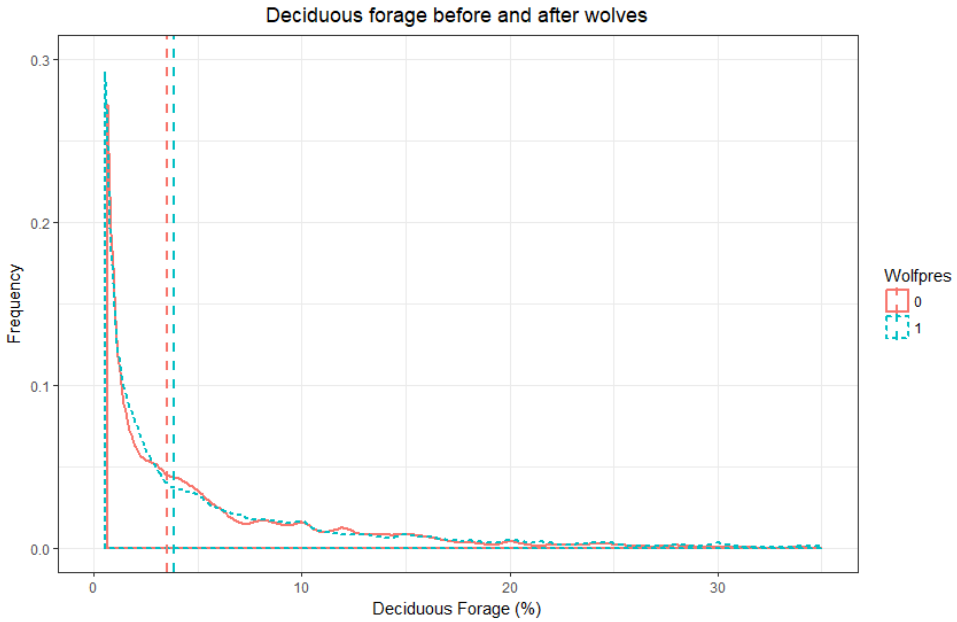

Figure 19. The distribution of deciduous forage before (red) and after (blue) wolf presence. Vertical dashed lines represent the average deciduous forage before and after wolf return

Proportion of days with snow cover >10cm

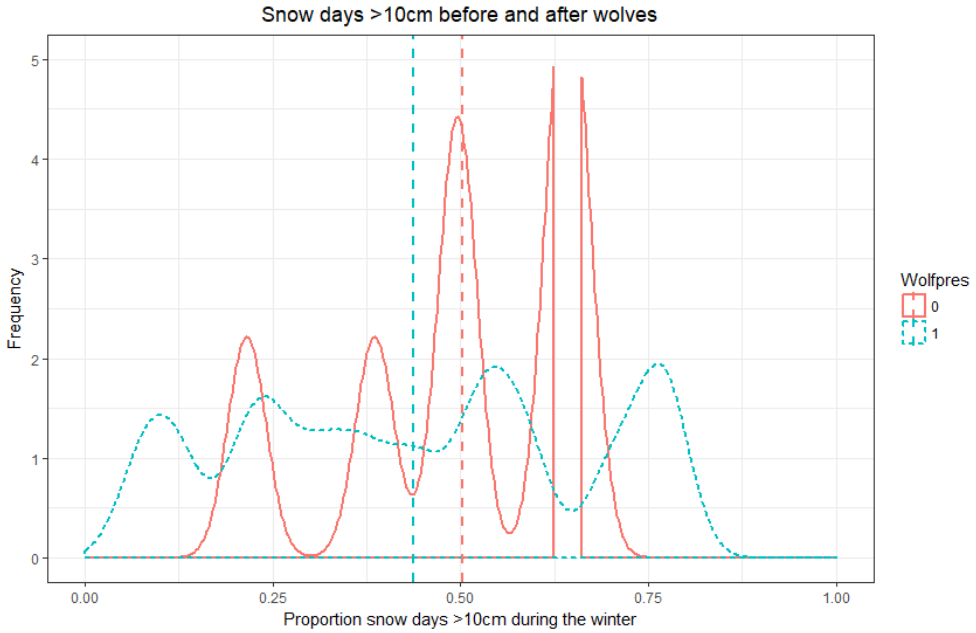

Figure 20. The proportion of snow days >10cm before (red) and after (blue) wolf presence. Vertical dashed lines represent the average proportion of snow days >10cm before and after wolf return

Moose density/square

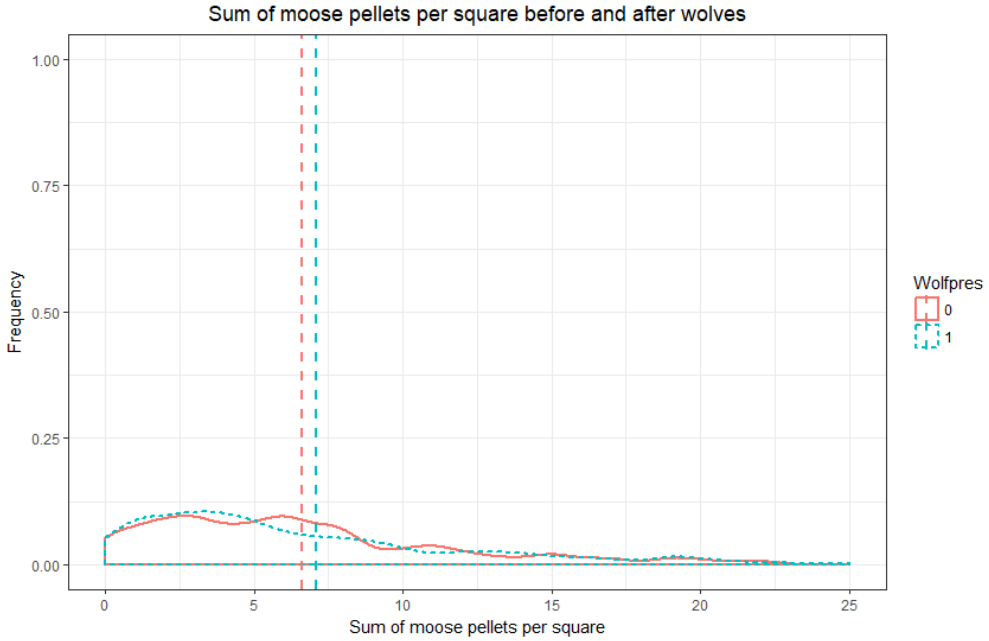

Figure 21. The distribution of total number of pellets found per square before (red) and after (blue) wolf presence. Vertical dashed lines represent the average moose pellet piles found before and after wolf return

4. *Habitat class availability before and after wolves*

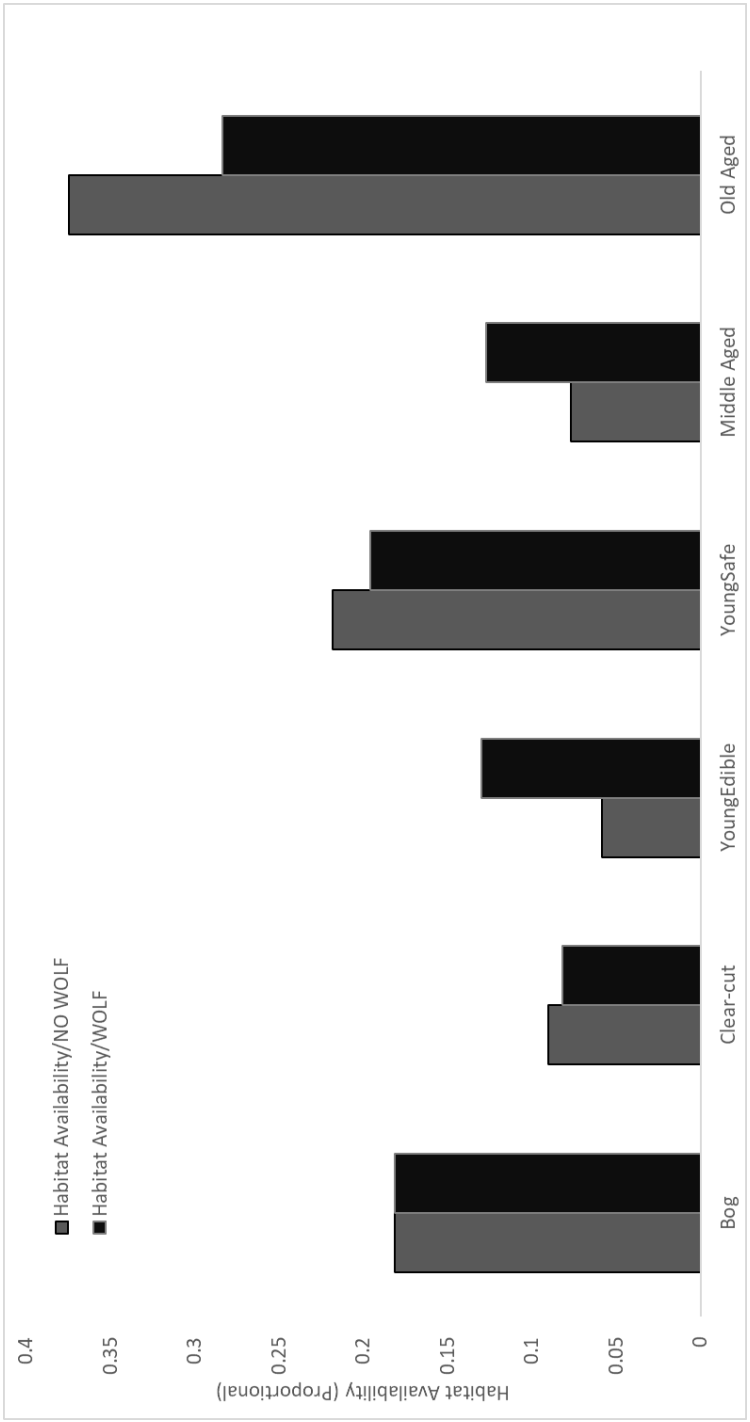

Figure 2211. The availability of each habitat class before and after wolves in the Grimsö Wildlife Research Area. The total number of plots with each habitat class was divided by the total number of plots used in the pellet group analysis.